

Transfer of *Streptococcus faecalis* and *Streptococcus faecium* to the Genus *Enterococcus* nom. rev. as *Enterococcus faecalis* comb. nov. and *Enterococcus faecium* comb. nov.

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The results of deoxyribonucleic acid-deoxyribonucleic acid and deoxyribonucleic acid-ribosomal ribonucleic acid hybridization studies demonstrated that *Streptococcus faecalis* and *Streptococcus faecium* are distantly related to the non-enterococcal streptococci (*Streptococcus bovis* and *Streptococcus equinus*) of serological group D and to other streptococci. On the basis of our results and those of previous studies, we propose that *S. faecalis* and *S. faecium* be transferred to the genus *Enterococcus* (ex Thiercelin and Jouhaud) nom. rev. as *Enterococcus faecalis* (Andrewes and Horder) comb. nov. and *Enterococcus faecium* (Orla-Jensen) comb. nov., respectively. A description of the genus *Enterococcus* nom. rev. and emended descriptions of *E. faecalis* and *E. faecium* are given.

The streptococci belonging to serological group D can be divided into two physiologically different groups. *Streptococcus faecalis* and *Streptococcus faecium* were placed in the enterococcus division of the streptococci, whereas *Streptococcus bovis* and *Streptococcus equinus* were placed in the viridans division by Sherman (21). Kalina proposed (9) that *Streptococcus faecalis* and *Streptococcus faecium* should be transferred to the genus "*Enterococcus*." This distinction between the enterococci and *Streptococcus bovis*, *Streptococcus equinus*, and other streptococci has also been demonstrated by comparative biochemical (25) and immunological (14, 15) studies. More recently, nucleic acid studies (7, 12) have confirmed that *Streptococcus faecalis* and *Streptococcus faecium* are only distantly related to *Streptococcus bovis* and *Streptococcus equinus*. In particular, deoxyribonucleic acid (DNA)-ribosomal ribonucleic acid (rRNA) homology studies (12) and comparative oligonucleotide cataloging of 16S rRNA (E. Seewaldt, Ph.D. thesis, Technische Universität München, Munich, Federal Republic of Germany, 1982) have indicated that the enterococcal and non-enterococcal group D streptococci belong to different genera. In this paper we extend these studies, and on the basis of the data we propose that *Streptococcus faecalis* and *Streptococcus faecium* be transferred to the genus *Enterococcus* (ex Thiercelin and Jouhaud) nom. rev. (22).

MATERIALS AND METHODS

The test strains which we used are listed in Table 1. The streptococci were cultivated in CASO-bouillon medium (E. Merck AG, Darmstadt, Germany) without aeration at 34°C. *Staphylococcus sciuri* and *Escherichia coli* were grown in shake flasks containing glucose-peptone-yeast extract broth (13) at 34°C. All strains were harvested in the exponential phase. The procedures used to prepare cell walls and determine the peptidoglycan types have been described previously (19, 20). Isolation of DNA and rRNA and nucleic acid hybridization experiments were carried out as described previously (11-13). The stability of DNA-rRNA hybrids is expressed by their melting temperatures. DNA base compositions were determined by thermal denaturation (16), using a Gilford model 2600 spectrophotometer. DNA from *Escherichia coli* K-12 was used as the standard. The guanine-plus-cytosine (G+C) contents were calculated by the method of

De Ley (4) and were corrected to the value for the reference *Escherichia coli* K-12 DNA.

RESULTS AND DISCUSSION

The DNA base compositions, serological groups, and peptidoglycan types of the test strains are shown in Table 1. The enterococci studied (*Streptococcus faecalis*, *Streptococcus faecium*, "*Streptococcus avium*", "*Streptococcus durans*", and "*Streptococcus casseliflavus*") had DNA G+C contents in the range from 37 to 43 mol%. These data are in good agreement with the data given recently by Farrow et al. (7); however, they are about 1 to 2 mol% lower than the values reported by Kilpper-Bälz et al. (12), who used a value for the base composition of the reference DNA that was too high (53 instead of 51.7 mol%).

Streptococcus faecalis and its subspecies possess the Lys-Ala_{2,3} peptidoglycan type and differ in this respect from all of the other enterococci, which contain the Lys-D-Asp peptidoglycan type (8, 12, 20). The results of previous studies, in particular those of Kilpper-Bälz et al. (12) and Seewaldt (Ph.D. thesis), clearly indicated that the enterococci are not closely related to the other streptococci. In this study ³H-labeled 23S rRNAs from *Streptococcus faecalis* DSM 20376 and "*Streptococcus avium*" DSM 20063 were hybridized with filter-bound DNAs from strains of *Streptococcus faecalis*, *Streptococcus faecium*, "*Streptococcus durans*", "*Streptococcus casseliflavus*", and some other streptococci (Table 2). Our results indicate that all of the enterococci examined share high rRNA homology and are only remotely related to other streptococci (Table 2).

The results of our DNA-DNA hybridization studies (Fig. 1) confirm the separate species status of *Streptococcus faecalis* and *Streptococcus faecium* (7, 12). All strains of *Streptococcus faecalis* were closely related (DNA homology values, 88%) regardless of their subspecies status. The *Streptococcus faecium* strains showed low but still significant levels of DNA homology (ca. 18%) with *Streptococcus faecalis*. The very low levels of DNA homology (<9%) between *Streptococcus faecalis* and *Streptococcus faecium* strains and other streptococci are consistent with the DNA-rRNA hybridization data (12). Three strains of *Streptococcus faecium* shared a lower level of DNA homology (40%) with the type strain of *Streptococcus faecium* (Fig. 1) and may represent a distinct species or at least a subspecies. The

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TABLE 1. Bacterial strains used and their serological groups, DNA base contents, and peptidoglycan types

Strain	Lancefield group	G+C content (mol%)	Type of peptidoglycan
" <i>Streptococcus avium</i> " DSM 20063	D+Q	39.2	Lys-D-Asp
" <i>Streptococcus bovis</i> " DSM 20480 ^{Ta}	D	38.0	Lys-Thr-Ala(Ser)
" <i>Streptococcus casseliflavus</i> " CCM 2478	D	43.7	Lys-D-Asp
" <i>Streptococcus casseliflavus</i> " CCM 2479	D	44.6	Lys-D-Asp
" <i>Streptococcus durans</i> " CCM 5612	D	39.0	Lys-D-Asp
" <i>Streptococcus durans</i> " Kiel 27382	D	38.2	Lys-D-Asp
" <i>Streptococcus faecalis</i> " DSM 20478 ^T	D	38.6	Lys-Ala ₂₋₃
" <i>Streptococcus faecalis</i> subsp. <i>faecalis</i> " DSM 20376	D	37.7	Lys-Ala ₂₋₃
" <i>Streptococcus faecalis</i> subsp. <i>faecalis</i> " Kiel 7067	D	37.7	Lys-Ala ₂₋₃
" <i>Streptococcus faecalis</i> subsp. <i>liquefaciens</i> " Kiel 26506	D	37.5	Lys-Ala ₂₋₃
" <i>Streptococcus faecalis</i> subsp. <i>zymogenes</i> " Kiel 20225	D	38.1	Lys-Ala ₂₋₃
<i>Streptococcus faecium</i> DSM 20477 ^T	D	39.0	Lys-D-Asp
<i>Streptococcus faecium</i> DSM 20160	D	37.4	Lys-D-Asp
<i>Streptococcus faecium</i> CCM 2123	D	38.6	Lys-D-Asp
<i>Streptococcus faecium</i> CCM 2308	D	38.1	Lys-D-Asp
<i>Streptococcus faecium</i> CCM 2423	D	38.0	Lys-D-Asp
<i>Streptococcus faecium</i> CCM 2424	D	37.5	Lys-D-Asp
<i>Streptococcus faecium</i> Kiel 26352	D	38.3	Lys-D-Asp
<i>Streptococcus lactis</i> DSM 20481 ^T	N	36.0	Lys-D-Asp
<i>Streptococcus mutans</i> ATCC 25175 ^T	Q	37.5	Lys-Ala ₂₋₃
<i>Streptococcus</i> species Kiel 9938 ^b	Q		Lys-D-Asp
<i>Streptococcus thermophilus</i> DSM 20479		38.3	Lys-Ala ₂₋₃
<i>Staphylococcus sciuri</i> ATCC 29062 ^T		33.6	Lys-Ala-Gly ₄₋₅
<i>Escherichia coli</i> DSM 30083		51.7	m-A ₂ pm-direct ^c

^a T = Type strain.

^b This strain is closely related to "*Streptococcus avium*" (M. D. Collins et al., Int. J. Syst. Bacteriol., in press).

^c m-A₂pm, meso-Diaminopimelic acid.

occurrence of *Streptococcus faecium* strains that differ genotypically from the type strain has also been reported by Farrow et al. (7).

On the basis of the results presented above and previously (1-3, 5, 7, 8, 10, 12, 17, 18, 20, 23-25), we propose that the species *Streptococcus faecalis* and *Streptococcus faecium* be reclassified as members of the genus *Enterococcus* (ex Thiercelin and Jouhaud) nom.rev. as *Enterococcus faecalis* comb.nov. and *Enterococcus faecium* comb.nov., respectively.

Description of the genus *Enterococcus* (ex Thiercelin and Jouhaud 1903). *Enterococcus* (En.te.ro.coc'cus. Gr. n. *enteron* intestine; Gr. n. *coccus* a grain, berry; M.L. masc. n. *Enterococcus* intestinal coccus) cells are ovoid, occur singly, in pairs, or in short chains, and are frequently elongated in the direction of the chain. Gram positive. Endospores are not formed. May be motile. Facultatively anaerobic. Optimum growth temperature, ca. 35°C. Strains grow at 10 and 45°C. Most strains survive heating at 60°C for 30 min. Grow in 6.5% NaCl and at pH 9.6. Hydrolyze pyrrolidonyl-β-naphthylamide. Chemoorganotrophs. Metabolism fermentative. The predominant end product of glucose fermentation is L-lactic acid. Oxygen or other hydrogen acceptors may

alter the end products of carbohydrate metabolism. Hydrogen peroxide may or may not accumulate in the presence of oxygen. Do not contain heme compounds. Benzidine negative and usually catalase negative, but some strains may produce pseudocatalase. Some strains synthesize cytochromes or catalase or both when they are provided with hemin. The minimal nutritional requirements are generally complex. React with group D antisera; some strains also react with group Q antisera.

Some strains possess respiratory quinones (menaquinones or demethylmenaquinones). Long-chain fatty acids are predominantly of the straight-chain saturated or monounsaturated types; some strains produce cyclopropane ring acids.

Peptidoglycan type: Lys-D-Asp or Lys-Ala₂₋₃.

The G+C content of the DNA ranges from 37 to 45 mol%.

Type species: *Enterococcus faecalis*.

Nucleic acid hybridization studies, in particular DNA-rRNA hybridization studies, demonstrate that members of the genus *Enterococcus* are closely related to each other but not to members of the genus *Streptococcus*. Enterococci can easily be differentiated from streptococci by their ability to

TABLE 2. Hybridization between ³H-labeled 23S rRNAs from *Streptococcus faecalis* DSM 20376 and "*Streptococcus avium*" DSM 20063 and filter-bound DNAs from different streptococci and other bacteria

Source of DNA	Melting temp (°C) after hybridization with ³ H-labeled rRNA from:	
	<i>Streptococcus faecalis</i> DSM 20376	" <i>Streptococcus avium</i> " DSM 20063
" <i>Streptococcus faecalis</i> subsp. <i>faecalis</i> " DSM 20376	80.0	ND ^a
" <i>Streptococcus faecalis</i> " DSM 20478	79.8	75.1
" <i>Streptococcus faecalis</i> subsp. <i>zymogenes</i> " Kiel 20225	79.2	ND
" <i>Streptococcus faecalis</i> subsp. <i>faecalis</i> " Kiel 7067	79.1	ND
" <i>Streptococcus faecalis</i> subsp. <i>liquefaciens</i> " Kiel 26506	78.0	ND
<i>Streptococcus faecium</i> DSM 20477 ^T	78.0	76.7
<i>Streptococcus faecium</i> DSM 20160	78.0	ND
<i>Streptococcus faecium</i> CCM 2423	77.4	77.2
<i>Streptococcus faecium</i> CCM 2424	77.4	ND
<i>Streptococcus faecium</i> CCM 2308	77.3	ND
" <i>Streptococcus casseliflavus</i> " CCM 2478	77.3	77.0
" <i>Streptococcus durans</i> " CCM 5612	77.1	ND
" <i>Streptococcus casseliflavus</i> " CCM 2479	76.6	76.3
<i>Streptococcus</i> species serology group Q Kiel 9938	76.5	79.8
" <i>Streptococcus faecium</i> " Kiel 26352	76.3	ND
" <i>Streptococcus avium</i> " DSM 20063	76.3	80.5
" <i>Streptococcus durans</i> " Kiel 27382	75.9	74.9
" <i>Streptococcus faecium</i> " CCM 2123	74.6	ND
<i>Streptococcus mutans</i> ATCC 25175 ^T	71.2	69.9
<i>Staphylococcus sciuri</i> ATCC 29062 ^T	71.0	70.5
<i>Streptococcus bovis</i> DSM 20480 ^T	70.9	70.0
<i>Streptococcus thermophilus</i> DSM 20479		70.5
<i>Streptococcus lactis</i> DSM 20481 ^T	68.7	67.8
<i>Escherichia coli</i> DSM 30083	63.4	

^a ND, Not determined.

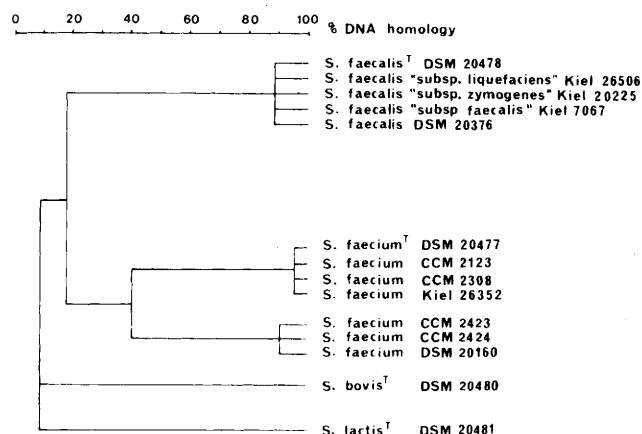


FIG. 1. Dendrogram based on DNA-DNA-homology. DNA hybridization studies were carried out under optimal conditions (25°C below the melting point of DNA).

grow in 6.5% NaCl and at pH 9.6. Moreover, in contrast to most streptococci (exceptions are *Streptococcus lactis*, *Streptococcus cremoris*, and *Streptococcus uberis*), they can grow at 10°C.

Description of *Enterococcus faecalis* (Andrews and Horder) comb. nov. The following description of *Enterococcus faecalis* (fae.'ci.'is. L.n. faex, dregs; N.L.adj. faecalis relating to feces) is based on the description given by Deibel and Seeley (3) and the studies of Schleifer and Kandler (20), Collins and Jones (2), Facklam and Wilkinson (6), Kilpper-Bälz et al. (12), and Farrow et al. (7).

Surface colonies on blood agar or nutrient agar are circular, smooth, and entire. Most strains are nonhemolytic; rarely, strains exhibit β -hemolysis. Ovoid cells elongated in the direction of the chain occur singly, in pairs, or in short chains. Usually nonmotile; rarely, strains are motile. Strains grow at 10 and 45°C, survive heating at 60°C for 30 min, and grow in 6.5% NaCl at pH 9.6 and in 0.1% methylene blue milk. Acid is produced from glycerol (under aerobic and anaerobic conditions), mannitol, sucrose, trehalose, D-tagatose, ribose, galactose, D-glucose, D-fructose, D-mannose, N-acetylglucosamine, salicin, cellobiose, maltose, lactose, β -gentiobiose, amygdalin, and arbutin. Acid is not produced from erythritol, D-arabinose, L-arabinose, α -methyl-xyloside, inositol, D-fucose, L-fucose, D-xylose, L-xylose, adonitol, L-sorbose, dulcitol, α -methyl-D-mannoside, α -methyl-D-glucoside, melibiose, inulin, D-raffinose, glycogen, xylitol, D-turanose, D-lyxose, D-arabitol, L-arabitol, and 5-keto-gluconate. Acid may be produced from rhamnose, sorbitol, melezitose, amidon, gluconate, and 2-keto-gluconate. The final pH in glucose broth is between 4.1 and 4.6.

Pyruvate is utilized as an energy source, as are citrate, malate, and serine. The utilization of the latter three substances is linked to pyruvate metabolism. Utilization of pyruvate, citrate, malate, and serine requires lipoate. Arginine and often agmatine are also utilized as energy sources. Strains do not require folic acid for growth in semidefined media.

Some strains produce a pseudocatalase. When grown aerobically, some strains possess a potent peroxidase and consequently do not accumulate hydrogen peroxide.

Growth occurs in the presence of 0.04% tellurite, which is reduced to tellurium, and in the presence of 0.01% tetrazolium, which is reduced to formazan. Growth occurs in the presence of 0.1% thallos acetate and 0.02% sodium azide.

Most strains decarboxylate tyrosine to tyramine plus carbon dioxide. Some strains hydrolyze gelatin, and some strains produce hyaluronidase. Most strains hydrolyze hippurate and esculin. Starch is not hydrolyzed.

The peptidoglycan type is Lys-Ala_{2,3} (10, 12, 20). The group-specific antigenic determinant (Lancefield group D) is a lipoteichoic acid in which glycerol residues are substituted with glucose and a D-alanine residue is linked to glucose (27, 28).

Most strains contain demethylmenaquinones with nine isoprene units as their major isoprenologs (2). Hexadecanoic, octadecenoic, and *cis*-11,12-methylenoctadecanoic acids are the major fatty acids.

The G+C content of the DNA ranges from 37 to 40 mol%.

The type strain is strain ATCC 19433 (= NCTC 775 = NCDO 581 = DSM 20478).

Description of *Enterococcus faecium* (Orla-Jensen) comb. nov. The following description of *Enterococcus faecium* (fae.'ci.um. L.n. faex, dregs; L.gen.pl.n. faecium of the dregs, of feces) is based on the description given by Deibel and Seeley (3) and the studies of Schleifer and Kandler (20), Collins and Jones (2), Kilpper-Bälz et al. (12), and Farrow et al. (7).

Surface colonies on blood agar or nutrient agar are circular, smooth, and entire. Nonpigmented. Some strains may produce an alpha-reaction on blood agar. Ovoid cells, elongated in the direction of the chain, occur chiefly in pairs or short chains. Some strains are motile. Strains grow at 10 and 50°C, survive heating at 60°C for 30 min, and grow in 6.5% NaCl and at pH 9.6. Acid is produced from ribose, galactose, D-glucose, D-fructose, D-mannose, N-acetylglucosamine, amygdalin, arbutin, salicin, cellobiose, maltose, lactose, β -gentiobiose, glycerol (only under aerobic conditions), L-arabinose, and trehalose. Acid is not produced from D-xylose, L-xylose, adonitol, L-sorbose, rhamnose, dulcitol, sorbitol, α -methyl-D-glucoside, inulin, melezitose, D-raffinose, amidon, glycogen, xylitol, D-turanose, D-lyxose, D-tagatose, D-arabitol, L-arabitol, 2-keto-gluconate, 5-keto-gluconate, erythritol, D-arabinose, α -methyl-xyloside, inositol, D-fucose, and L-fucose. Acid may be produced from mannitol, α -methyl-D-mannoside, melibiose, sucrose, and gluconate. The final pH in glucose broth is 4.0 to 4.4.

Pyruvate, citrate, malate, and serine are not utilized as sources of energy for growth. Ammonia is produced from arginine, but it is not used as an energy source. Hippurate and esculin are hydrolyzed. Gelatin is not hydrolyzed. Hydrogen peroxide may accumulate in the presence of oxygen.

TABLE 3. Differentiation of *Enterococcus faecalis* and *Enterococcus faecium*

Characteristic	<i>Enterococcus faecalis</i>	<i>Enterococcus faecium</i>
Peptidoglycan type	Lys-Ala _{2,3}	Lys-D-Asp
Menaquinones	DMK-9	-
Acid produced from:		
Arabinose	-	+
Tagatose	+	-
Energy from:		
Pyruvate	+	-
Citrate	+	-
Malate	+	-
Serine	+	-
Reduction of:		
0.04% Tellurite	+	-
0.01% Tetrazolium	+	-

Growth occurs in the presence of 0.1% thallos acetate and 0.02% sodium azide. Tellurite (0.04%) is not reduced to tellurium, nor is tetrazolium (0.01%) reduced to formazan.

The peptidoglycan type is Lys-D-Asp (10, 12, 20). Cells contain neither menaquinones nor ubiquinones (2). Hexadecanoic, octadecenoic, and *cis*-11,12-methylenoctadecanoic acids are the major fatty acids (7).

The G+C content of the DNA ranges from 37 to 40 mol%.

The type strain is strain ATCC 19434 (= NCTC 7171 = NCDO 942 = DSM 20477).

The differential characteristics of the two species described above are listed in Table 3.

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