Enterococcus avium nom. rev., comb. nov.; *E. casseliflavus* nom. rev., comb. nov.; *E. durans* nom. rev., comb. nov.; *E. gallinarum* comb. nov.; and *E. malodoratus* sp. nov.

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Biochemical, chemical, and genetic data indicate that strains labeled *Streptococcus avium* (Nowlan and Deibel), "*Streptococcus casseliflavus*" (Vaughn, Riggsby and Mundt), "*Streptococcus durans*" (Sherman and Wing), "*Streptococcus faecalis* subsp. *malodoratus*" (Pette), and *Streptococcus gallinarum* (Bridge and Sneath) are closely related to members of the genus *Enterococcus* Schleifer and Kilpper-Bälz. We propose that these taxa be classified as members of the genus *Enterococcus*, as *Enterococcus avium* nom. rev., comb. nov., *Enterococcus casseliflavus* nom. rev., comb. nov., *Enterococcus durans* nom. rev., comb. nov., *Enterococcus malodoratus* sp. nov., and *Enterococcus gallinarum* comb. nov., respectively.

The inclusion of *Streptococcus faecalis* and *Streptococcus faecium* in the genus *Streptococcus* has been controversial for some time (12). Kalina (14) proposed that these species be transferred to the genus "*Enterococcus*" of Thiercelin and Jouhaud (25). However, this proposal was not generally accepted, and the genus *Enterococcus* was not recognized in *Bergey's Manual of Determinative Bacteriology*, 8th ed. (5). Recent nucleic acid studies (10, 15, 21) have indicated that *S. faecalis* and *S. faecium* are quite distinct from the majority of the species in the genus *Streptococcus*. Consideration of these data led Schleifer and Kilpper-Bälz (21) to repropose the transfer of *S. faecalis* and *S. faecium* to the genus *Enterococcus* (ex Thiercelin and Jouhaud) Schleifer and Kilpper-Bälz.

In addition to *S. faecalis* and *S. faecium*, a number of other streptococci conform to the characteristics of the enterococcus division of Sherman (22). These include "*Streptococcus avium*" (18), "*Streptococcus casseliflavus*" (26), "*Streptococcus durans*" (23), "*S. faecalis* subsp. *malodoratus*" (19), and "*S. faecium* subsp. *mobilis*" (16), none of which were included on the Approved Lists of Bacterial Names (24), as well as the recently described species *Streptococcus gallinarum* (3). Recent deoxyribonucleic acid (DNA)-DNA and DNA-ribosomal ribonucleic acid studies in our laboratories (10, 15, 21) have shown that these taxa are closely related to *Enterococcus faecalis* and *Enterococcus faecium* but only distantly related to other streptococci. The same studies also have indicated that with the exception of "*S. faecium* subsp. *mobilis*" the taxa listed above are sufficiently distinct (less than 30% DNA-DNA homology under stringent hybridization conditions) from each other to be considered separate species (10). Strains designated "*S. faecium* subsp. *mobilis*" have been shown to be members of the species "*S. casseliflavus*" (76 to 97% DNA-DNA homology under optimum conditions) (10). On the basis of biochemical, chemical, and genetic data (3, 6, 10, 13, 15, 20, 21, 26), we believe that "*S. avium*," "*S. casseliflavus*," "*S. durans*," "*S. faecalis* subsp. *malodoratus*," and *S. gallinarum* should be transferred to the genus *Enterococcus* as distinct species.

The purpose of this paper is to propose the classification

of these taxa as *Enterococcus avium* nom. rev., comb. nov., *Enterococcus casseliflavus* nom. rev., comb. nov., *Enterococcus durans* nom. rev., comb. nov., *Enterococcus malodoratus* sp. nov., and *Enterococcus gallinarum* comb. nov., respectively. The physiological, biochemical, chemical, and genetic characteristics of the type strains and representative strains of all of these species have been published previously by us and other workers (1–4, 6, 10, 11, 15–21, 23, 26).

The strains of all of the species conform in the main to the characteristics of the genus *Enterococcus* (ex Thiercelin and Jouhaud) Schleifer and Kilpper-Bälz. They are all gram-positive, facultatively anaerobic, catalase-negative cocci which occur mostly in pairs or short chains; grow at 10°C and, unless otherwise stated below, at 45°C; survive heating at 60°C for 30 min; grow in 6.5% (wt/vol) NaCl, at pH 9.6, and in 40% (vol/vol) bile; and produce L-lactic acid as the major end product of glucose fermentation.

***Enterococcus avium*.** The following description of *Enterococcus avium* (ex Nowlan and Deibel 1967) nom. rev., comb. nov. (av.i'um. L.n. avis bird; L.gen. pl. *avium* of birds) is based on previous descriptions (6, 9, 10, 13, 18, 20, 21). Ovoid cells elongated in the direction of the chain, mostly in pairs or short chains. Nonmotile. Surface colonies on blood agar or nutrient agar are circular, smooth, and entire. Nonpigmented. Most strains produce an alpha-reaction on blood agar. No requirement for riboflavin or pyridoxal in casein hydrolysate medium. Folinic acid (or folic acid plus thymine) is required for growth. Amino acid requirements not known. Arginine and starch are not hydrolyzed. H₂S produced. Acetylmethylcarbinol not produced. Nitrate is not reduced. Does not grow in the presence of 0.04% tellurite or in 0.1% methylene blue milk. Other biochemical characteristics are given in Table 1. Reacts with Lancefield group D antisera and also usually, but not always, with Lancefield group Q antisera.

Group A peptidoglycan based upon lysine (type, Lys-D-Asp). Respiratory quinones absent. The major non-hydroxylated long-chain fatty acids are tetradecanoic (C_{14:0}) and hexadecanoic (C_{16:0}) acids; octadecenoic (C_{18:1}) and *cis*-11,12-methylenoctadecanoic (ΔC_{19:0}) acids are present in only small amounts (less than 5%). Isolated from human, animal, and chicken feces. The guanine-plus-cytosine content of the DNA ranges from 39 to 40 mol%, as determined

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TABLE 1. Differential biochemical characteristics of *E. avium*, *E. casseliflavus*, *E. durans*, *E. faecium*, *E. faecalis*, *E. malodoratus*, and *E. gallinarum*^a

Characteristic	<i>E. avium</i>	<i>E. durans</i>	<i>E. faecalis</i>	<i>E. faecium</i>	<i>E. malodoratus</i>	<i>E. casseliflavus</i>	<i>E. gallinarum</i>
Acid produced from: ^b							
Adonitol	+	—	—	—	+	—	—
Amidon	—	—	—(w+)	—	—	—(w+)	+
L-Arabinose	+	—	—	+	—	+	+
D-Arabitol	+	—	—	—	+	—	—
L-Arabitol	+	—	—	—	+	—	—
Dulcitol	+	—	—	—	+	—	—
Glycerol	+	—	+	+	v	—	+
Glycogen	—	—	—	—	—	—	—(+)
Gluconate	+(—)	—	+(—)	v	+	+	+
Inulin	—	—	—	—	—	+	+
2-Keto-gluconate	+	—	v	—	+	—	—
5-Keto-gluconate	v	—	—	—	—	—	—
D-Lyxose	+	—	—	—	—	—	—
Mannitol	+	—(+)	+	+(—)	+	+	+
Melezitose	+	—	+(—)	—	—	—	—
Melibiose	—	—	—	v	+	+	+
α-Methyl-D-mannoside	+(—)	—	—	—(+)	+	+(—)	—
α-Methyl-D-glucoside	+	—	—	—	—	+	+
D-Raffinose	—	—	—	—	+	—	+
Rhamnose	+	—	v	—	+	+(—)	—
Sorbitol	+	—	+(—)	—	+	—	+
L-Sorbose	+	—	—	—	+	—	—
Sucrose	+	—	+	v	+	+	+
D-Tagatose	+	—	+	—	+	—	+
Trehalose	+	+(—)	+	+	+	+	+
D-Turanose	+	—	—	—	v	v	+
Xylitol	+	—	—	—	+	—	—
D-Xylose	—	—	—	—	v	+	+
L-Xylose	—	—	—	—	v	—	—
Hydrolysis of: ^d							
Esculin	+	+	+(—)	+	+	+	+
Hippurate	v	v	+(—)	+	v	—	+
Production of: ^d							
Arginine dehydrolase	—	+	+	+	—	+(—)	+
α-Galactosidase	—	—	—	—	+	+	+
β-Galactosidase	v	v	—	+	+	+	+
β-Glucuronidase	—	—	—	—	—	—	+

^a The following strains were tested: *E. avium* NCDO 2366, NCDO 2367, NCDO 2368, NCDO 2369^T, and NCDO 2370; *E. durans* NCDO 498, NCDO 593, and NCDO 596^T; *E. faecalis* NCDO 581, NCDO 584, NCDO 586, NCDO 588, NCDO 610, and NCDO 611; *E. faecium* NCDO 502, NCDO 503, NCDO 594, NCDO 942, and NCDO 944; *E. malodoratus* NCDO 846^T and NCDO 847; *E. casseliflavus* NCDO 2372^T, NCDO 2376, NCDO 2378, NCDO 2380, NCDO 2154, and NCDO 2310; and *E. gallinarum* NCDO 2311, NCDO 2313^T, NCDO 2314, and NCDO 2315. All strains produced acid from *N*-acetylglucosamine, amygdalin, arbutin, cellobiose, D-fructose, galactose, β-gentiobiose, D-glucose, lactose, maltose, D-mannose, ribose, and salicin. All strains failed to produce acid from D-arabinose, erythritol, D-fucose, L-fucose, inositol, and α-methyl-xyloside.

^b As determined with the API 50CH system, using bromocresol purple (0.002%, wt/vol) as the indicator in 1% (wt/vol) peptone water.

^c +, Positive; —, negative; v, variable; +(—), most strains positive but occasional strains negative; —(+), most strains negative but occasional strains positive; —(w+), most strains negative but occasional strains weakly positive.

^d Hippurate, esculin, and enzymatic tests were performed with the API 20S system according to the instructions of the manufacturer.

by melting temperature. The strains form a distinct homology group, as determined by DNA-DNA hybridization (10). The type strain is NCDO 2369 (= Guthof E6844 = ATCC 14025). This strain was isolated from human feces (11).

Description of the type strain. In most respects the description of the type strain resembles the description of the species. Positive reactions are obtained with Lancefield group Q and group D antisera. Acid is produced from gluconate and from α-methyl-D-mannoside. Strain NCDO 2369^T (T = type strain) produces β-galactosidase and hydrolyzes hippurate (Table 1).

E. avium strains form a distinct species on the basis of genomic (10) and biochemical criteria (10, 18) (Table 1). *E. avium* and *E. malodoratus* are the only species of the genus *Enterococcus* that are known to produce H₂S (detected by

lead acetate paper inserted into slopes of cultures on blood agar base no. 2 [Oxoid] medium supplemented with 0.05% [wt/vol] cysteine hydrochloride). However, in contrast to *E. malodoratus*, *E. avium* strains grow well at 45°C and survive heating at 60°C for 30 min. In addition, they may be distinguished by their fermentation patterns and by the production of α-galactosidase (*E. malodoratus* produces this compound but *E. avium* does not). *E. malodoratus* never reacts with Lancefield group Q antisera.

***Enterococcus casseliflavus*.** The following description of *Enterococcus casseliflavus* (ex Vaughn, Riggsby and Mundt 1979) nom. rev., comb. nov. (cass.el.i.flavus. M.L. n. casseli of Cassel [Cassel yellow]; L.adj. flavus yellow; casseliflavus yellow colored) is based on previous descriptions (1, 6, 10, 16, 17, 21, 26). Coccoid cells usually in pairs

or short chains. Motile. Surface colonies on blood agar or nutrient agar are circular, smooth, and entire. Yellow pigment produced. Acetylmethylcarbinol produced. Gray, punctate colonies on agar supplemented with 0.04% potassium tellurite. H₂S not produced. No decarboxylation of tyrosine. Other biochemical properties are given in Table 1. Reacts with Lancefield group D antisera.

Group A peptidoglycan based upon lysine (type, Lys-D-Asp). Menaquinones present, with MK-7 and MK-8 as the major isoprenologues (6). The major non-hydroxylated long-chain fatty acids are hexadecanoic (C_{16:0}) and octadecenoic (C_{18:1}) acids; *cis*-11,12-methylenoctadecanoic acid (Δ C_{19:0}) either is absent or is present in only trace amounts.

Isolated from plants, silage, and soil. The guanine-plus-cytosine content of the DNA ranges from 40.5 to 44.9 mol%, as determined by melting temperature. The strains form a distinct homology group, as determined by DNA-DNA hybridization (10). The type strain is ATCC 25788 (= NCDO 2372 = MUTK 20). This strain was isolated from plant material (26).

Description of the type strain. In most respects the description of the type strain corresponds with the description of the species. Acid is not produced from amidon. Acid is produced from α -methyl-D-mannoside, rhamnose, and D-turanose (Table 1).

In many phenotypic characters *E. casseliflavus* resembles *E. faecium*, but strains of *E. casseliflavus* may be distinguished from *E. faecium* by some biochemical tests (Table 1), by the production of a bright yellow pigment, and by the possession of respiratory quinones (6).

***Enterococcus durans*.** The following description of *Enterococcus durans* (ex Sherman and Wing 1937) nom. rev., comb. nov. (du'rans. L.part.adj. *durans* hardening, resisting) is based on previous descriptions (6-8, 10, 13, 15, 20, 23). Ovoid cells elongated in the direction of the chain, chiefly in pairs or short chains. Surface colonies on blood agar or nutrient agar are circular, smooth, and entire. Nonpigmented. Some strains produce an alpha-reaction on blood agar; a few strains are beta-hemolytic. Nonmotile. Nutritionally exacting; amino acids and B vitamins are required for growth in synthetic media. Grows on 0.1% methylene blue milk. No growth in media containing 0.04% tellurite and 0.01% tetrazolium. H₂S is not produced. Other biochemical characteristics are given in Table 1. Reacts with Lancefield group D antisera.

Group A peptidoglycan based upon lysine (type, Lys-D-Asp). Respiratory quinones absent. The major non-hydroxylated long-chain fatty acids are hexadecanoic (C_{16:0}) and octadecenoic (C_{18:1}) acids; substantial amounts of *cis*-11,12-methylenoctadecanoic (Δ C_{19:0}) acid are also present (approximately 10%).

Isolated from milk and dairy products. The guanine-plus-cytosine content of the DNA ranges from 38 to 40 mol%, as determined by melting temperature. There is approximately 40% homology with the DNA of the type strain of *E. faecium* under optimum hybridization conditions; this value decreases to approximately 20% under stringent conditions (10). The type strain is NCDO 596 (= ATCC 19432 = 98D). This strain was isolated from dried milk (23).

Description of the type strain. The type strain differs from most other members of the species by exhibiting beta-hemolysis on horse blood (5%, vol/vol) agar plates. It does not produce acid from mannitol or trehalose, nor does it hydrolyze hippurate. It does produce β -galactosidase (Table 1).

On the basis of phenotypic characters, it is not easy to

distinguish strains of *E. durans* from *E. faecium*. Indeed, it has been suggested that on the basis of phenotypic criteria the two taxa should be combined (9, 12). However, the data of Jones et al. (13) show that strains labeled *S. faecium* and "*S. durans*" occupy a large area of phenetic space, with "*S. durans*" strains showing a closer similarity to each other than to *S. faecium* strains. Strains of *E. faecium* are more saccharolytic than strains of *E. durans* (Table 1). In addition, strains of *E. faecium* grow in nutrient broth no. 2 (Oxoid) supplemented with 0.1% glucose incubated at 50°C. *E. durans* strains do not grow at 50°C. These differences, combined with the low level of DNA homology (40% under optimum conditions) (10), are in our view sufficient to designate strains formerly named "*S. durans*" (Sherman and Wing) as a separate species, *E. durans*.

***Enterococcus gallinarum*.** The following description of *Enterococcus gallinarum* (ex Bridge and Sneath 1982) comb. nov. (gall.in.ar'um. L.fem.gen. pl.n. *gallinarum* of hens) is based on previous descriptions (2, 3, 10). Coccoid cells, mostly in pairs or short chains. Nonmotile. Colonies on blood agar or nutrient agar are circular, smooth, and entire. Beta-hemolytic on horse blood agar (2). Nonpigmented. Most strains do not survive heating at 60°C for 30 min (2) but survive heating at 60°C for 15 min (3). Grows slowly on thallous acetate-tetrazolium agar at room temperature, producing deep pink colonies (2). Ammonia produced from L-arginine. Gelatin not liquefied. H₂S not produced. Other biochemical characteristics are given in Table 1. Reacts with Lancefield group D antisera.

Group A peptidoglycan based upon lysine (type, Lys-D-Asp). Low levels of menaquinones produced, with MK-8 predominating. The major non-hydroxylated long-chain fatty acids are hexadecanoic (C_{16:0}) and octadecenoic (C_{18:1}) acids; *cis*-11,12-methylenoctadecanoic acid (Δ C_{19:0}) is present in small amounts.

Isolated from intestines of domestic fowls. The guanine-plus-cytosine content of the DNA ranges from 39 to 40 mol%, as determined by melting temperature. The strains form a distinct homology group, as determined by DNA-DNA hybridization (10). The type strain is NCTC 11428 (= NCDO 2313 = F87/276). This strain was isolated from a chicken intestine (2).

Description of the type strain. The characteristics of the type strain are the same as those described above for the species. Acid is not produced from glycogen.

Strains of *E. gallinarum* may be confused with those strains of *E. faecalis* and *E. durans* which are beta-hemolytic on horse blood agar. However, *E. gallinarum* differs from members of these species in a number of important respects (see above; Table 1).

***Enterococcus malodoratus*.** The following description of *Enterococcus malodoratus* (ex Pette 1955) sp. nov. (mal.od.or.a'tus. M.L. n. *malus* ill; M.L.n. *odoratus* odor; *mal-odoratus* ill smelling) is based on previous descriptions (6, 10, 13, 19) and our observations. Coccoid cells, mostly in pairs or short chain. Nonmotile. Some strains produce slime. Colonies on blood agar or nutrient agar are circular, smooth, and entire. Usually does not grow at 45°C. Usually does not survive heating at 60°C for 30 min. Nonpigmented. Acetylmethylcarbinol not produced. H₂S produced. Other biochemical characteristics are given in Table 1. Reacts with Lancefield group D antisera.

Group A peptidoglycan based upon lysine (type, Lys-D-Asp). Respiratory quinones absent. The major non-hydroxylated long-chain fatty acids are tetradecanoic (C_{14:0}) and hexadecanoic (C_{16:0}) acids; octadecenoic acid (C_{18:1}) and *cis*-

11,12-methylenoctadecanoic ($\Delta C_{19:0}$) acids are present in small amounts (less than 10%).

Isolated from Gouda cheese. The guanine-plus-cytosine content of the DNA ranges from 40 to 41 mol%, as determined by melting temperature. The strains form a distinct homology group, as determined by DNA-DNA hybridization. This species exhibits approximately 50% homology with *E. avium* under optimum hybridization conditions; under stringent conditions the homology values with *E. avium* are less than 20% (10).

The type strain is strain NCDO 846, which was isolated from Gouda cheese (19).

Description of the type strain. The type strain does not grow at 45°C or survive heating at 60°C for 30 min. No acid is produced from glycerol, D-turanose, D-xylose, or L-xylose. Hippurate is not hydrolyzed (Table 1).

Strains of *E. malodoratus* are most likely to be confused with strains of *E. avium* since both produce H₂S, do not hydrolyze arginine, and produce acid from a number of polyols; these properties are not shared with other enterococci. However, *E. malodoratus* strains may be distinguished from *E. avium* strains by a number of phenotypic characteristics (see above; Table 1).

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