NOTES

16S rRNA Gene Similarities Indicate that *Hallella seregens* (Moore and Moore) and *Mitsuokella dentalis* (Haapasalo et al.) Are Genealogically Highly Related and Are Members of the Genus *Prevotella*: Emended Description of the Genus *Prevotella* (Shah and Collins) and Description of *Prevotella dentalis* comb. nov.

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Because of similarities in the cellular fatty acid compositions of *Hallella seregens* and *Mitsuokella dentalis*, we determined the 16S rRNA gene sequences of the type strains of these species to assess their relationship. A very high level of sequence relatedness (approximately 99.8%) was found between *H. seregens* and *M. dentalis*, indicating that these species are genealogically closely related. A comparative sequence analysis revealed that these two species are members of the genus *Prevotella* and are phylogenetically remote from *Mitsuokella multiacidus* (the type species of the genus *Mitsuokella*), which was found to be a member of the *Sporomusa* subbranch of the *Clostridium* subphylum of the gram-positive bacteria. On the basis of our phylogenetic findings, we propose that *M. dentalis* should be reclassified as *Prevotella dentalis* comb. nov.

Recently, Moore and Moore (12) described a group of anaerobic, gram-negative, rod-shaped bacteria that were isolated from the gingival crevices of humans with gingivitis or periodontitis. These authors proposed the name *Hallella seregens* gen. nov., sp. nov. for this group, which was formerly referred to as “*Bacteroides* D12” (12). The genome of *H. seregens* has a high G+C content (58 mol%), like *Mitsuokella multiacidus* (56 to 58 mol%) and *Rikenella microfus* (60 to 61 mol%) (12). Unlike *M. multiacidus* and *R. microfus*, *H. seregens* contains iso-C_{14:0} and iso-C_{16:0} fatty acids, and it does not contain iso-C_{15:0} as *R. microfus* does or C_{12:0} and C_{16:1cis7} as *M. multiacidus* does (10). Because of this distinctive cellular fatty acid pattern and the fact that this organism is much more fermentative than *R. microfus*, a separate genus and species, *H. seregens*, was proposed for “*Bacteroides* D12” (12).

An inspection of previous reports (4, 5) revealed similarities in the cellular fatty acid patterns of *H. seregens* and *Mitsuokella dentalis*, a species described for isolates obtained from human dental root canals (5). The genus *Mitsuokella* was created on the basis of morphological, biochemical, and chemotaxonomic criteria to accommodate *Bacteroides multiacidus*, which contained gram-negative, anaerobic, saccharolytic, rod-shaped isolates obtained from human and animal feces (15, 17). *M. dentalis* differs from *M. multiacidus* in many phenotypic properties, including acid end products, carbohydrate fermentation reactions, starch hydrolysis, resistance to bile, and cellular fatty acid composition (4, 15). The phylogenetic positions of *M. multiacidus* (the type species of the genus) and *M. dentalis* are unknown, and there are no genotypic data, apart from similar G+C contents, that support inclusion of these species in a single genus. To investigate the phylogenetic relationships of

H. seregens and both *Mitsuokella* species, we determined the sequences of the 16S rRNA genes of the type strains and performed a comparative sequence analysis.

H. seregens ATCC 51272^T (T = type strain), *M. multiacidus* NCTC 10934^T, and *M. dentalis* DSM 3688^T were obtained from the American Type Culture Collection, Rockville, Md., the National Collection of Type Cultures, London, United Kingdom, and the Deutsche Sammlung von Mikroorganismen und Zellkulturen, Braunschweig, Germany, respectively. The lyophilized cells were resuspended in 500 µl of TES buffer (0.05 M Tris-HCl, 0.005 M EDTA, 0.05 M NaCl; pH 8.0), and DNA was extracted by the method of Lawson et al. (9). The almost complete 16S rRNA gene of each organism was amplified by a PCR by using primers directed to conserved positions proximal to the 5' end (primer ARI; 5'-GAGAGTTTGATCCTGGCTCAGGA; *Escherichia coli* positions 7 to 29) and 3' end (primer pH*; 5'-AAGGAGGTGATCCAGCCGCA; *E. coli* positions 1541 to 1522) of the gene as described previously (8). The amplified products were purified by using a Prep-A-Gene kit (Bio-Rad, Hercules, Calif.) and were sequenced by using a *Taq* DyeDeoxy Terminator Cycle Sequencing Kit (Applied Biosystems, Inc., Foster City, Calif.) and an automated sequencer (model 373A; Applied Biosystems Inc.). To establish the closest known relatives of the sequences determined, searches of the EMBL and GenBank data libraries were performed by using the program FASTA (2). The new sequences were aligned with their closest relatives by using the program PILEUP (2), and the alignment was corrected manually. For the phylogenetic analysis approximately 100 bases were omitted from the 5' end of the gene because of alignment ambiguities in variable region V1. A distance matrix was calculated by using the program DNADIST (with the Kimura-2 parameter) of the PHYLIP package (3). A phylogenetic tree was drawn by using the neighbor-joining method and the program NEIGHBOR (3). Using the programs SEQBOOT, DNADIST,

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TABLE 1. Representative similarity values for the 16S rRNA genes of *H. seregens* and *M. dentalis* and their relatives

Taxon	% Similarity with:																	
	<i>Haletella sergens</i>	<i>Mitsuokella dentalis</i>	<i>Prevotella bivia</i>	<i>Prevotella buccae</i>	<i>Prevotella buccalis</i>	<i>Prevotella corporis</i>	<i>Prevotella denticola</i>	<i>Prevotella distens</i>	<i>Prevotella intermedia</i>	<i>Prevotella loescheii</i>	<i>Prevotella melaninogenica</i>	<i>Prevotella nigrescens</i>	<i>Prevotella oralis</i>	<i>Prevotella oris</i>	<i>Prevotella ouloris</i>	<i>Prevotella ruminicola</i>	<i>Prevotella veroralis</i>	<i>Bacteroides fragilis</i>
<i>Mitsuokella dentalis</i>	99.8																	
<i>Prevotella bivia</i>	90.3	90.2																
<i>Prevotella buccae</i>	89.7	89.7	88.7															
<i>Prevotella buccalis</i>	88.8	88.8	90.2	89.3														
<i>Prevotella corporis</i>	90.0	90.0	91.2	89.5	90.5													
<i>Prevotella denticola</i>	90.1	90.0	89.8	91.4	89.1	90.7												
<i>Prevotella disiens</i>	87.9	87.9	92.0	87.4	89.8	92.0	89.6											
<i>Prevotella intermedia</i>	89.0	88.9	91.1	88.0	89.0	92.5	89.8	93.6										
<i>Prevotella loescheii</i>	90.8	90.7	90.3	90.4	90.6	90.6	90.6	88.8	89.8									
<i>Prevotella melaninogenica</i>	89.7	89.6	92.7	89.1	89.2	92.7	93.6	91.9	91.5	90.6								
<i>Prevotella nigrescens</i>	89.7	89.6	90.7	88.9	90.0	93.0	91.2	91.8	94.1	90.3	91.5							
<i>Prevotella oralis</i>	89.1	89.1	89.4	89.2	90.9	88.7	88.7	87.6	87.5	91.0	89.4	88.8						
<i>Prevotella oris</i>	90.1	90.2	91.8	90.2	91.4	91.0	91.4	89.8	90.6	91.1	92.0	90.7	89.2					
<i>Prevotella ouloris</i>	90.2	90.3	92.1	89.3	90.2	92.5	91.6	93.2	91.6	90.3	93.7	91.0	89.3	93.1				
<i>Prevotella ruminicola</i>	86.8	86.8	90.1	87.4	89.0	88.4	88.2	88.4	88.1	88.4	89.8	87.7	88.1	88.7	89.2			
<i>Prevotella veroralis</i>	89.7	89.7	92.3	89.5	89.2	92.1	92.4	91.6	91.0	90.0	97.0	90.7	88.4	91.9	93.8	89.4		
<i>Bacteroides fragilis</i>	81.7	81.6	84.6	82.3	82.9	83.6	82.3	84.1	82.9	82.6	84.2	83.5	81.9	82.6	85.2	83.6	83.2	
<i>Porphyromonas asaccharolytica</i>	78.8	78.8	79.9	79.2	78.5	79.7	78.0	79.5	78.5	78.8	79.4	78.3	77.8	78.9	80.8	78.7	79.4	81.6

NEIGHBOR, and CONSENSE (3), we assessed the stability of the groups by bootstrapping.

for the groups by bootstrapping. The 16S rRNA gene sequences of *H. seregens* ATCC 51272^T, *M. dentalis* DSM 3688^T, and *M. multiacidus* NCTC 10934^T which we determined consisted of 1,463, 1,482, and 1,511 nucleotides, respectively. The 16S rRNA genes of *H. seregens* and *M. dentalis* exhibited a very high level of sequence similarity (99.8%). Although such a high level of 16S rRNA relatedness does not necessarily imply species identity, it is evident from this result that *H. seregens* and *M. dentalis* are genealogically closely related and are either members of the same species or members of two closely related genomic species. Phenotypically, the two species are very similar, and the only reported differences are fermentation of trehalose and hydrolysis of starch by *H. seregens* but not by *M. dentalis* (5, 12). Chromosomal DNA-DNA pairing is necessary to ascertain whether *H. seregens* and *M. dentalis* are different species. A comparative 16S rRNA sequence analysis revealed that *H. seregens* and *M. dentalis* are phylogenetically most closely related to *Prevotella* species in the *Bacteroides-Flavobacterium* phylum of gram-negative bacteria. Sequence similarity values of approximately 87 to 91% were obtained with members of the genus *Prevotella*; these values were similar to the values found when different *Prevotella* species were compared (Table 1). Topologically, the treeing program which we used placed *H. seregens* and *M. dentalis* well within the confines of the genus *Prevotella* (Fig. 1). All of the signature positions in the 16S rRNA reported for *Prevotella* species (13) were present in both *H. seregens* and *M. dentalis*. In contrast, *M. multiacidus* exhibited much lower levels of sequence relatedness with *M. dentalis* (level of similarity, approximately 71%) and related gram-negative taxa (data not shown). Far higher levels of sequence similarity were found between *M. multiacidus* and members of the *Sporomusa* subbranch of the *Clostridium* subphylum of gram-positive bacteria. The highest levels of sequence relatedness were observed with *Selenomonas* species (91.5 to 96.1%)

(Table 2). The results of the treeing program are shown in Fig. 2. These results clearly show that *M. multiacidus* belongs in the *Sporomusa* subbranch, whose members are gram negative. It is evident from both the distances and tree branching that *M. multiacidus* exhibits a specific association with *Selenomonas ruminantium* (bootstrap value, 100) (Fig. 2). Although it is not possible to derive fixed sequence divergence values for circumscribing or delineating genera, there is no doubt from our findings that *M. multiacidus* is closely related to the selenomonads. It is worth noting that *M. multiacidus* differs phenotypically from *Selenomonas* species in a number of important traits. The discriminating features include the distinctive fatty acid pattern of *M. multiacidus* (13), the lack of the tumbling mobility and flagella typical of selenomonads in *M. multiacidus* (6, 15), and the fact that when *M. multiacidus* ferments glucose, it produces mainly acetic and lactic acids and moderate amounts of succinic acid (17), whereas *Selenomonas* strains produce acetic and propionic acids, CO₂, and/or lactate (1). In view of the phenotypic differences described above and the general genealogical complexities in the *Sporomusa* lineage, more *Selenomonas* species must be analyzed before conclusions regarding the precise taxonomic status of *M. multiacidus* can be made with confidence.

It is clear from the results of our comparative 16S rRNA analysis that the genus *Mitsuokella* is not a monophyletic group and that *M. dentalis* is phylogenetically a member of the genus *Prevotella*. It should also be noted that *M. dentalis* is phenotypically not dissimilar from *Prevotella* species; one possible difference is the absence of menaquinones in *M. dentalis* (4). The G+C content of *M. dentalis* (56 to 60 mol%) is higher than the G+C contents reported for the genus *Prevotella* (40 to 52 mol% [16]). However, there are no absolute boundary conditions for genera when G+C content criteria are used. It should be noted that members of other phylogenetically coherent genera exhibit similar, if not greater, G+C content ranges (e.g., the G+C contents of members of the genus *Corynebacterium*).

FIG. 1. Unrooted phylogenetic tree showing the position of *H. seregens* and *P. dentalis* within the *Bacteroides*-*Prevotella*-*Porphyromonas* subgroup of the *Flavobacterium*-*Cytophaga* phylum of gram-negative bacteria. Bootstrap values greater than 80 are shown at the branch points; bootstrap values of ≥ 90 are considered significant.

terium sensu stricto range from 46 to 70 mol%). Although the level of sequence divergence (approximately 12%) and the G+C content range (40 to 60 mol%) are somewhat high, there is no simple way of subdividing the genus *Prevotella* without a major proliferation of genera. This would be difficult to justify phenotypically and undesirable taxonomically. Therefore, on the basis of our findings, we formally propose that the species *M. dentalis* (Haapasalo et al. 1986) should be reclassified in the emended genus *Prevotella* (Shah and Collins 1990) as *Prevotella dentalis* comb. nov. It is also evident from the data presented above that *H. seregens* is genealogically very closely related to *P. dentalis*. However, DNA-DNA pairing studies will be necessary to establish whether *H. seregens* also represents a new *Prevotella* species or is a later subjective synonym of *P. dentalis*.

Description of *Prevotella* (Shah and Collins 1990) emend. The description below is based on that given in reference 16. Gram-negative, obligately anaerobic, non-spore-forming, non-motile, pleomorphic rods. Surface colonies on blood agar plates vary from minute to 2.0 mm in diameter and are generally circular, entire, convex, shiny, and smooth. Colonies on blood agar are translucent, opaque, and grey, light brown, or black. Hemolysis is variable. Glucose broth cultures are usually turbid with smooth or stringy sediments, and the terminal pH is between 4.5 and 5.2. The level of glucose utilization varies between 30 and 90% in BM broth. The optimum temperature for growth is 37°C, but some strains grow at 25 and 45°C.

Growth of most species is inhibited by 6.5% NaCl. Hemin and menadione are required for growth of most species. Growth is inhibited by 20% (wt/vol) bile. The major fermentation products from BM medium or peptone-yeast extract-glucose medium are acetic and succinic acids; occasionally lower levels of isobutyric, isovaleric, or lactic acid are produced. Malate dehydrogenase and glutamate dehydrogenase are present; glucose-6-phosphate dehydrogenase and 6-phosphogluconate dehydrogenase are absent. Proteolytic activity is variable. Most species have limited abilities to ferment amino acids. Nearly all species are indole negative. Nitrate is not reduced to nitrite. The cell wall peptidoglycan contains *meso*-diaminopimelic acid. Respiratory menaquinones (principally MK-10 to MK-13) may or may not be present. Both nonhydroxylated and 3-hydroxylated fatty acids are present. The nonhydroxylated fatty acids are composed of predominantly straight-chain saturated, anteiso- and iso-methyl, branched-chain types. Sphingolipids are produced. The DNA base compositions are within the approximate range from 40 to 60 mol% G+C. The type species is *Prevotella melaninogenica*.

Description of *Prevotella dentalis* (Haapasalo et al. 1986) comb. nov. The description below is based on that given by Haapasalo et al. (4, 5). Cells are nonmotile, non-spore-forming, gram-negative, blunt-ended, oval rods that are 0.7 by 1 to 2 μ m. They occur singly. Peritrichous fimbriae and a thick capsule-like structure are present. Obligately anaerobic. Poor

TABLE 2. Representative similarity values for the 16S rRNA genes of *M. multiacidus* and members of the *Sporomusa* subbranch of the gram-positive bacteria

Taxon	% Similarity with:														
	<i>Mitsuokella multiacidus</i>	<i>Acidaminococcus fermentans</i>	<i>Clostridium quercicolum</i>	<i>Dialister pneumosintes</i>	<i>Megasphaera elsdenii</i>	<i>Pectinatus cerevisiophilus</i>	<i>Pectinatus frisingensis</i>	<i>Phascolarobacterium faecium</i>	<i>Quinella ovalis</i>	<i>Selenomonas lactificex</i>	<i>Selenomonas ruminantium</i> subsp. <i>lactilytica</i>	<i>Selenomonas ruminantium</i> subsp. <i>ruminantium</i>	<i>Selenomonas sputigena</i>	<i>Sporomusa paucivorans</i>	<i>Sporomusa termitida</i>
<i>Acidaminococcus fermentans</i>	87.6														
<i>Clostridium quercicolum</i>	88.8	86.2													
<i>Dialister pneumosintes</i>	86.8	84.9	83.8												
<i>Megasphaera elsdenii</i>	86.2	84.9	86.4	88.5											
<i>Pectinatus cerevisiophilus</i>	89.2	85.4	88.1	85.2	86.4										
<i>Pectinatus frisingensis</i>	88.5	84.1	86.8	84.4	86.4	95.0									
<i>Phascolarobacterium faecium</i>	87.7	90.6	88.2	83.9	85.7	86.2	84.8								
<i>Quinella ovalis</i>	85.3	82.8	84.0	81.8	81.9	83.9	83.4	83.7							
<i>Selenomonas lactificex</i>	93.3	87.7	90.3	85.0	86.2	89.0	88.4	87.4	84.9						
<i>Selenomonas ruminantium</i> subsp. <i>lactilytica</i>	95.8	87.1	88.4	85.9	85.9	89.1	88.1	87.1	86.0	93.8					
<i>Selenomonas ruminantium</i> subsp. <i>ruminantium</i>	96.1	87.3	88.6	85.9	85.8	89.4	88.4	87.1	85.7	93.9	98.9				
<i>Selenomonas sputigena</i>	91.5	86.8	88.3	84.8	85.4	88.7	88.9	86.5	85.5	90.0	91.0	90.9			
<i>Sporomusa paucivorans</i>	87.7	87.6	90.0	84.3	84.6	88.1	86.3	89.1	82.8	88.6	87.0	87.1	86.2		
<i>Sporomusa termitida</i>	85.2	85.5	88.0	81.4	83.3	86.0	85.2	86.9	81.4	86.9	85.6	85.5	84.6	93.2	
<i>Veillonella atypica</i>	86.5	86.2	87.0	87.2	89.4	86.7	85.7	86.2	81.6	87.6	86.8	86.8	85.6	86.3	84.0
<i>Veillonella dispar</i>	86.5	85.9	87.0	88.8	89.8	86.7	84.8	86.1	82.2	87.6	87.2	87.0	85.7	86.2	84.3
<i>Veillonella parvula</i>	86.4	86.3	86.9	87.7	89.6	87.0	85.6	86.1	81.9	87.4	87.0	86.6	85.6	85.9	84.2
<i>Zymophilus paucivorans</i>	89.7	86.3	89.0	84.0	85.9	88.2	88.4	86.4	82.4	91.9	89.8	89.8	88.5	88.2	86.6

growth occurs in liquid media; better growth occurs on blood agar media supplemented with hemolyzed blood. No growth occurs on kanamycin-vancomycin laked blood agar. After 3 days, colonies on enriched horse blood agar (containing hemolyzed blood) are 1 to 2 mm in diameter, convex, irregular, translucent, wet, and mucoid; they have a characteristic water drop appearance. Alpha-hemolysis on horse and sheep blood agar usually occurs after 7 days of incubation.

Ferments arabinose, cellobiose, fructose, galactose, glucose, lactose, maltose, mannose, and raffinose in prereduced anaer-

bically sterilized peptone-yeast extract broth. Melibiose and sucrose are weakly fermented (pH 5.5 to 5.7). Erythritol, mannitol, melezitose, rhamnose, salicin, and xylose are not fermented. Fermentation reactions are negative as determined by API 20A systems. No hydrolysis of gelatin and starch occurs. Esculin hydrolysis is negative in esculin broth for anaerobes, but positive when a chromogenic substrate for the detection of a constitutive enzyme is used with cells grown on an agar plate. The major metabolic end products are acetate and succinate. Malate dehydrogenase is present, and glutamate

FIG. 2. Unrooted phylogenetic tree showing the position of *M. dentalis* within the *Sporomusa* subbranch of the *Clostridium* subphylum of the gram-positive bacteria. Bootstrap values greater than 80 are shown at the branch points; bootstrap values of ≥ 90 are considered significant.

TABLE 3. Characteristics that differentiate *P. dentalis* and other *Prevotella* species^a

Species	Acid produced from:							Hydrolysis of:		Pigment production on blood agar
	Arabinose	Cellobiose	Lactose	Mannose	Raffinose	Salicin	Xylose	Esculin	Gelatin	
<i>P. dentalis</i>	+	+ ^b	+	+	+	—	—	+	—	—
<i>P. bivia</i>	—	—	+	+	—	—	—	—	+	—
<i>P. buccae</i>	+	+	+	+	+	+	+	+	+	—
<i>P. buccalis</i>	—	+	+	+	+	+	—	+	—	—
<i>P. corporis</i>	—	—	—	+	—	—	—	—	+	+
<i>P. denticola</i>	—	v	+	+	+	v	—	+	+	v
<i>P. disiens</i>	—	—	—	—	—	—	—	—	+	—
<i>P. enoea</i>	—	—	+	v	—	—	v	v	+	—
<i>P. heparinolytica</i>	+	+	+	+	—	+	+	+	—	—
<i>P. intermedia</i>	—	—	—	v	v	—	—	—	+	+
<i>P. loeschii</i>	—	+	+	+	+	v	—	+	+	+
<i>P. melaninogenica</i>	—	v	+	+	+	—	—	v	+	+
<i>P. oralis</i>	—	+	+	+	+	+	+	+	+	—
<i>P. oris</i>	+	+	+	+	+	+	—	+	v	—
<i>P. oulora</i>	—	—	+	+	+	—	—	+	—	—
<i>P. ruminicola</i>	+	+	+	+	+	+	v	+	+	—
<i>P. tanneriae</i>	—	—	v	v	v	—	—	v	+	v
<i>P. veroralis</i>	—	v	+	+	+	v	v	+	v	—
<i>P. zoogloformans</i>	v	v	v	v	v	v	v	+	v	—

^a Data from references 5, 7, 11, 14, and 18.^b +, positive reaction; —, negative reaction; v, different reactions reported by different authors.

dehydrogenase is present in minor amounts. α -Arabinosidase, α -galactosidase, α -glucosidase, β -galactosidase, β -glucosidase, β -N-acetylglucosaminidase, alkaline phosphatase, and alanine aminopeptidase are present. Hydrolyzes indoxylacetate. α -Fucosidase, α -mannosidase, and β -glucosidase are absent. Does not produce leucine, proline, tyrosine, arginine, histidine, phenylalanine, and glycine aminopeptidases or pyroglutamic acid arylamidase. Arginine is not utilized.

Resistant to kanamycin and colistin. Vancomycin is inhibitory at concentrations higher than 5 μ g/ml. Susceptible to erythromycin, penicillin, rifampin, and metronidazole and to oxgall and brilliant green.

Cell walls contain *meso*-diaminopimelic acid as the dibasic amino acid and glycine, alanine, glutamic acid, and aspartic acid. Hydroxylated and nonhydroxylated long-chain fatty acids are present; 3-OH-C_{16:0} is the main hydroxylated fatty acid, and C_{16:0} and iso-C_{14:0} are the major fatty acids. The G+C content of the DNA ranges from 56 to 60 mol% (as determined by thermal denaturation).

Isolated from dental root canals. The type strain is strain DSM 3688.

P. dentalis can be distinguished from other *Prevotella* species by the typical water drop appearance of its colonies on solid media (5) and by the characteristics listed in Table 3.

The 16S rRNA gene sequences of *H. seregens* ATCC 51272^T, *P. dentalis* DSM 3688^T, and *M. multiacidus* NCTC 10934^T have been deposited in the EMBL data library under accession numbers X81877, X81876, and X81878, respectively.

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