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Glucose 6-Phosphate Dehydrogenase and 6-Phosphogluconate Dehydrogenase Activities and Glucose Utilization by Species within the Genera *Bacteroides*, *Prevotella*, and *Porphyromonas*

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Members of the genera *Bacteroides*, *Prevotella*, and *Porphyromonas* were investigated for their glucose 6-phosphate dehydrogenase (G6PDH) and 6-phosphogluconate dehydrogenase (6PGDH) activities by using spectrophotometric (SP) and alloenzyme elecrophoresis (AE) detection methods. When the SP and AE methods were compared, the AE method failed to detect activity in two of the six strains which exhibited G6PDH and 6PGDH activities as determined by the SP detection method. On the basis of the results of SP detection, *Bacteroides levii* ATCC 29147^T (T = type strain) (G6PDH and 6PGDH negative) is not a member of the genus *Bacteroides* as currently defined, which reflects recent 16S rRNA placement, nor do *Prevotella heparinolytica* ATCC 35895^T, *Prevotella zoogleoformans* ATCC 33285^T, *Porphyromonas canoris* 12835^T, and *Porphyromonas salivosa* NCTC 11632^T (all G6PDH and 6PGDH positive) conform to their respective genus descriptions. When these organisms were grown in prereduced peptone-yeast extract broth containing 10% (wt/vol) glucose, the amounts of glucose remaining after 5 days were less than the amounts present initially for members of the genus *Bacteroides* (*Bacteroides fragilis* ATCC 25285^T and *B. levii*) and members of the genus *Prevotella* (*Prevotella melaninogenica* ATCC 25845^T, *Prevotella buccae* ATCC 33574^T, *Prevotella heparinolytica*, and *Prevotella zoogleoformans*). In addition, the glucose levels were lower after 5 days of incubation in broth media containing *Porphyromonas asaccharolytica* ATCC 25845^T and *Porphyromonas salivosa*, but not in media containing the other members of the genus *Porphyromonas* tested (*Porphyromonas canoris*, *Porphyromonas circumdentaria* NCTC 12469^T, *Porphyromonas endodontalis* ATCC 35406^T, and *Porphyromonas gingivalis* ATCC 33277^T). The reductions in glucose levels were not directly related to the final pH values. Our results suggest that the descriptions of the genera *Bacteroides*, *Prevotella*, and *Porphyromonas* may require emendation to reflect variability in G6PDH and 6PGDH activities and glucose utilization.

The genus *Bacteroides* as described in *Bergey's Manual of Systematic Bacteriology* (5) contains a heterogeneous collection of species (11). This has led to nomenclature changes, including the establishment of the genus *Porphyromonas* for the "asaccharolytic pigmented *Bacteroides* spp." (12) and the establishment of the genus *Prevotella* for the "moderately saccharolytic, predominately oral *Bacteroides* spp." (14). In addition, the description of the genus *Bacteroides* has been emended so that this genus contains "only the saccharolytic, bile tolerant strains" (13). Since these changes, workers have published 16S rRNA sequence data which have shown that some species currently classified in the genera *Bacteroides* and *Prevotella* do not cluster with other members of these genera (10). In the descriptions of the redefined genera, the methods used to determine whether organisms were saccharolytic, moderately saccharolytic, or asaccharolytic were not specified. However, the descriptions included references to studies in which workers used acidification or failure to acidify media containing carbohydrates and/or changes in glucose concentrations as the determinants for defining organisms as saccharolytic or asaccharolytic (5, 17). A literal definition of a saccharolytic organism is an organism that is capable of breaking down carbohydrate(s). Acids may be produced from substances other than carbohydrates (e.g., amino acids, purines, pyrimidines), and metabolites (e.g., ammonia) may affect the final pH values of media. Therefore, a lower terminal pH does not necessarily indicate that carbohydrates are broken down and cannot be used alone as an indicator of saccharolytic activity.

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One of the components of the emended descriptions of the genera *Bacteroides*, *Prevotella*, and *Porphyromonas* was whether glucose 6-phosphate dehydrogenase (G6PDH) and 6-phosphogluconate dehydrogenase (6PGDH) activities were present (12–14). The inclusion of these dehydrogenase activity characteristics was based on studies (11, 16) in which workers used a spectrophotometric (SP) method to detect dehydrogenase activity and alloenzyme electrophoresis (AE) to determine the electrophoretic mobilities in strains that exhibited dehydrogenase enzyme activity when the SP technique was used. These workers concluded that members of the genus *Bacteroides* exhibit both G6PDH and 6PGDH activities, while members of the genera *Porphyromonas* and *Prevotella* did not exhibit either enzyme activity at detectable levels. However, valid descriptions of some *Prevotella* and *Porphyromonas* species either have not included dehydrogenase activity data (1, 9, 20) or have included dehydrogenase activity data based only on AE results (6, 15). However, there apparently have been no reports of comparisons of the SP and AE detection methods, and thus it is not known if the two techniques give identical results. In this paper we describe a comparison of *Bacteroides*, *Prevotella*, and *Porphyromonas* species in which the SP and AE techniques were used to determine G6PDH and 6PGDH activities. We also examined the association between the final pH values of glucose-based media and the ability of selected *Bacteroides*, *Prevotella*, and *Porphyromonas* species to break down glucose.

MATERIALS AND METHODS

Bacterial strains. The strains which we used were *Bacteroides fragilis* ATCC 25285^T (T = type strain) and *Bacteroides levii* ATCC 29147^T, which were obtained from the American Type Culture Collection; *Prevotella melaninogenica* VPI 2381^T (= ATCC 25845^T), which was obtained from L. V. H. Moore;

TABLE 1. G6PDH and 6PGDH activities of selected *Bacteroides*, *Prevotella*, and *Porphyromonas* strains as determined by the SP and AE methods[a]

Strain[b]	Enzyme activities			
	SP method (nmol mg of protein^{-1} min^{-1})		AE method[c]	
	G6PDH	6PGDH	G6PDH	6PGDH
Bacteroides fragilis ATCC 25285^T	96	36	+	+
Prevotella heparinolytica ATCC 35895^T	20	18	−	−
Prevotella zoogleoformans ATCC 33285^T	30	6	ND[d]	ND
Porphyromonas canoris NCTC 12835^T	66	63	+	+
Porphyromonas canoris VPB 4879	58	38	+	+
Porphyromonas canoris VPB 4882	41	62	+	+
Porphyromonas salivosa NCTC 11632^T	48	14	−	−

[a] When we used the SP method, we did not detect G6PDH and 6PGDH activities in *B. levii* ATCC 29147^T, *Prevotella melaninogenica* ATCC 25845^T, *Prevotella bivia* ATCC 29303^T, *Prevotella buccae* ATCC 33574^T, *Prevotella buccalis* ATCC 35310^T, *Prevotella corporis* ATCC 33547^T, *Prevotella disiens* ATCC 29426^T, *Prevotella intermedia* ATCC 25611^T, *Prevotella loescheii* ATCC 15930^T, *Prevotella oralis* ATCC 33269^T, *Prevotella oris* ATCC 33573^T, *Prevotella veroralis* ATCC 33779^T, *Porphyromonas asaccharolytica* ATCC 25260^T, and *Porphyromonas endodontalis* ATCC 35406^T. G6PDH and 6PGDH activities were not detected in *Porphyromonas circumdentaria* NCTC 12469^T and *Porphyromonas gingivalis* ATCC 33277^T, VPB 3318, and VPB 3492 by the SP and AE methods.

[b] ATCC, American Type Culture Collection; NCTC, National Collection of Type Cultures; VPB, Veterinary Pathology and Bacteriology.

[c] +, enzyme activity band detected; −, enzyme activity band not detected.

[d] ND, not done.

Prevotella zoogleoformans VPI D28K-1^T (= ATCC 33285^T), which was obtained from the late E. P. Cato; *Prevotella bivia* ATCC 29303^T, *Prevotella corporis* ATCC 33547^T, *Prevotella disiens* ATCC 29426^T, *Prevotella intermedia* ATCC 25611^T, and *Prevotella heparinolytica* ATCC 35895^T, which were obtained from the American Type Culture Collection; *Prevotella buccae* CCUG 15401^T (= ATCC 33574^T), *Prevotella buccalis* CCUG 15557^T (= ATCC 35310^T), *Prevotella loescheii* CCUG 5914^T (= ATCC 15930^T), *Prevotella oralis* CCUG 15408^T (= ATCC 33269^T), *Prevotella oris* CCUG 15405^T (= ATCC 33573^T), and *Prevotella veroralis* CCUG 15422^T (= ATCC 33779^T), which were obtained from the Culture Collection of the University of Göteborg; *Porphyromonas asaccharolytica* ATCC 25268^T and *Porphyromonas gingivalis* ATCC 33277^T, which were obtained from the American Type Culture Collection; and *Porphyromonas salivosa* VPB 157^T (= NCTC 11632^T), *Porphyromonas circumdentaria* VPB 3329^T (= NCTC 12469^T), feline strains *Porphyromonas gingivalis* VPB 3318 and VPB 3492 (7), *Porphyromonas canoris* VPB 4878^T (= NCTC 12835^T), *Porphyromonas canoris* VPB 4879 and VPB 4882 (8), and *Porphyromonas endodontalis* CCUG 16442^T (= ATCC 35406^T), which were obtained from the Culture Collection of the University of Göteborg.

Preparation of bacterial extracts. The general methods used for growth were the methods described by Holdeman et al. (4). Cells were harvested following 16 h of growth in prereduced brain heart infusion broth (4) supplemented with 4 ml of salts solution (4) per liter and 0.47% (wt/vol) glucose or following 2 to 3 days of growth on sheep blood agar supplemented with hemin-menadione, formate fumarate, and Proteose Peptone (6). The cells were washed twice with cold (5°C) distilled water and stored at −140°C. The cells were lysed by sonication at 4°C with a model 375 sonicator (Heat Systems Ultrasonics, Inc.) (cup horn power output, 6) for 6 min or by passing them twice through a cold French pressure cell (Aminco model Fa-030) at 110 MPa. Following lysis, preparations were centrifuged at 17,000 × *g* for 20 min in a refrigerated (5°C) centrifuge to remove cellular debris.

SP determination of G6PDH and 6PGDH activities. We used the SP method of Deutsch (3), with some modifications. Briefly, G6PDH activity was measured at 340 nm with maleimide (an inhibitor of 6PGDH) in the reaction mixture by using a Gilford model 260 spectrophotometer at 37°C. Negative controls in which distilled water was substituted for substrate were included. The 6PGDH assay was performed like the G6PDH assay except that maleimide was omitted from the assay mixture and 6-phosphogluconate was used as the substrate. The activity values reported below were the averages of the values from three separate assays per preparation and were determined by using an extinction coefficient for NADPH of 6.22×10^2. The Bio-Rad protein assay (Bio-Rad, Richmond, Calif.) was used as recommended by the manufacturer to determine the protein concentration of each preparation; bovine serum albumin was used as the protein standard.

AE. AE was performed with selected isolates as described previously (6). Extracts were applied to gels by placing approximately 1 μl of bacterial extract containing 6 to 7 mg of protein per ml on a gel as a single line. Gels were read at 15 min to determine enzyme activity band formation.

Utilization of glucose and pH values of glucose-containing media (final pH values and changes in pH values). Glucose utilization was determined for the type species of the genera *Bacteroides*, *Prevotella*, and *Porphyromonas* and for selected other species belonging to these genera (see Table 2). For each strain, three single colonies were inoculated into cooked meat medium (bovine viande-foie broth [19] containing chopped meat, cysteine, and hemin-menadione [4]) and grown for 18 to 24 h at 37°C. Each broth preparation was checked for purity by Gram staining and was inoculated into two tubes containing prereduced peptone-yeast extract-glucose broth (PYG) (4). Immediately following inoculation, each tube was vortexed for 20 s. We let each tube stand for 20 s, and then a 3-ml aliquot was removed. The pH of the aliquot was determined (this was the initial pH), the aliquot was centrifuged at 12,000 × *g* for 20 min, and the supernatant was removed. This supernatant was mixed by vortexing, and three 100-μl aliquots were removed, mixed with equal volumes of distilled water, and then stored at −20°C until they were assayed for their glucose contents. The inoculated tubes were incubated at 37°C for 7 days, Gram stained, and subcultured aerobically to check for purity before the frozen aliquots were assayed. A negative control consisted of PYG inoculated with sterile cooked meat medium and processed as described above. Glucose levels were determined with a Cobas Mira instrument (Hoffman-La Roche Diagnostics, Basle, Switzerland) by using an enzymatic glucose reagent (hexokinase) (Trace Scientific, Clayton, Australia) as described by the manufacturer.

RESULTS

The results of SP determinations of enzyme activities are presented in Table 1. *B. fragilis* exhibited G6PDH and 6PGDH activities of 96 and 36 nmol mg of protein^{-1} min^{-1}, respectively, while 2 of 13 *Prevotella* spp. exhibited G6PDH activities of 20 and 30 nmol mg of protein^{-1} min^{-1} and 6PGDH activities of 6 and 18 nmol mg of protein^{-1} min^{-1}. Four of the 10 members of the genus *Porphyromonas* tested exhibited G6PDH activities which ranged from 41 to 66 nmol mg of protein^{-1} min^{-1} and 6PGDH activities which ranged from 14 to 63 nmol mg of protein^{-1} min^{-1}. G6PDH and 6PGDH activities were not detected in extracts of *B. levii*, 11 of the 13 *Prevotella* strains tested, and 6 of the 10 *Porphyromonas* strains tested.

Table 1 also shows the results of a comparison of the SP and AE methods for detecting G6PDH and 6PGDH activities. When the AE method was used, activity was not discernible until more than 0.27 U of G6PDH (1 U was defined as the amount of enzyme which converted 1 μmol of NADP to NADPH in 1 min) or 0.11×10^{-3} U of 6PGDH was applied to the gel. When we increased the enzyme detection time (to more than 30 min), we observed weak bands with *Prevotella heparinolytica*, *Prevotella zoogleoformans*, and *Porphyromonas salivosa*. However, in our hands this procedure increased the potential for development of staining artifacts which could be reported as false-positive reactions in strains for which no activity was detected when the SP method was used.

The results of tests for glucose utilization and pH following growth in PYG are shown in Table 2. We found that the

TABLE 2. Utilization of glucose and final pH values following incubation of selected *Bacteroides*, *Prevotella*, and *Porphyromonas* strains in PYG

Strain[a]	Glucose in PYG			Final pH of PYG	pH change
	Initial concn (nmol/liter)	Final concn (nmol/liter)	% Reduction		
Bacteroides fragilis ATCC 25285^T	32	16	50	5.3	1.4
Bacteroides levii ATCC 29147^T	33	14	58	5.6	1.0
Prevotella melaninogenica ATCC 25845^T	28	7	75	4.8	1.9
Prevotella buccae ATCC 33574^T	31	6	81	4.6	2.1
Prevotella heparinolytica ATCC 35895^T	34	18	47	5.6	1.0
Prevotella zoogleoformans ATCC 33285^T	35	10	71	5.6	0.9
Porphyromonas asaccharolytica ATCC 25260^T	32	19	41	6.2	0.5
Porphyromonas circumdentaria NCTC 12469^T	32	33	0	6.3	0.3
Porphyromonas canoris NCTC 12835^T	32	32	0	6.6	0
Porphyromonas endodontalis ATCC 35406^T	29	32	0	6.6	0
Porphyromonas gingivalis ATCC 33277^T	31	37	0	6.6	0
Porphyromonas salivosa NCTC 11632^T	33	13	60	5.9	0.7

[a] ATCC, American Type Culture Collection; NCTC, National Collection of Type Cultures.

amounts of glucose that remained after 5 days of growth were less than the amounts present initially for all *Bacteroides* spp. and *Prevotella* spp. tested. The glucose levels were also lower after 5 days of incubation in broth media containing *Porphyromonas asaccharolytica* (32 to 19 mmol/liter) and *Porphyromonas salivosa* (33 to 13 mmol/liter) but not in media containing the other *Porphyromonas* spp. tested.

Table 2 shows the final pH values in PYG. Incubation of *B. fragilis* for 5 days reduced the pH of the medium by 1.4 pH units to a final pH of 5.3, and incubation of *B. levii* reduced the pH of the medium by 1.0 pH unit to a final pH of 5.6. Members of the genus *Prevotella* likewise reduced the pH values of PYG by 0.9 to 2 pH units, with final pH values ranging from 4.6 to 5.7. However, *Porphyromonas* strains either caused no change in the pH (final pH value range, 6.3 to 6.6) or produced changes of 0.5 and 0.7 pH unit (final pHs, 6.2 and 5.9, respectively).

DISCUSSION

Basic to the nomenclature of the anaerobic, gram-negative, rod-shaped bacteria have been descriptions in which the so-called saccharolytic activities and G6PDH and 6PGDH activities of strains have been used. Using the SP method to detect these enzyme activities, we obtained results that were similar to those of Shah and Williams (16) for the six strains common to our report and the report of Shah and Williams despite quantitative differences in G6PDH and 6PGDH enzyme activities. When the SP and AE methods were compared, however, the AE method failed to detect activity in two of the six strains which exhibited G6PDH and 6PGDH activities as determined by the SP method (Table 1). While some workers have reported G6PDH and 6PGDH activities on the basis of AE data, our results suggest that only the SP technique should be used to detect these activities until a simple, more reliable technique becomes available. On the basis of SP detection, *B. levii* (G6PDH and 6PGDH negative) is not a member of the genus *Bacteroides* as currently defined, nor do *Prevotella heparinolytica*, *Prevotella zoogleoformans*, *Porphyromonas canoris*, and *Porphyromonas salivosa* (all G6PDH and 6PGDH positive) conform completely to their respective genus descriptions (Table 1). This brings into question the usefulness of G6PDH and 6PGDH activities as key determinants of species identity in the genera *Bacteroides*, *Prevotella*, and *Porphyromonas* as currently defined. Alternately, placement of these species in their current genera is not valid.

Table 2 shows that the final pH was not necessarily a direct indication of saccharolytic activity. For example, *B. fragilis*, *Prevotella buccae*, *Prevotella melaninogenica*, *Prevotella heparinolytica*, *Prevotella zoogleoformans*, *Porphyromonas asaccharolytica*, and *Porphyromonas salivosa* cultures exhibited decreases in the levels of measurable glucose ranging from 41 to 81%. While the decreases in the pH values of the media ranged from 0.5 pH unit (*Porphyromonas asaccharolytica*) to 2.1 pH units (*Prevotella buccae*), these decreases were not consistent with the reductions in measurable glucose levels, nor were they correlated with the current division into saccharolytic, moderately asaccharolytic, and asaccharolytic taxa. Given that the final pH is the result of a range of activities (utilization of carbohydrate is only one potential activity), these findings suggest that workers need to be careful when they interpret a change in the pH of peptone-carbohydrate medium as indicating that carbohydrate utilization has occurred. Our results illustrate that the current primary division of the genera *Bacteroides*, *Prevotella*, and *Porphyromonas* based on final pH values in carbohydrate media after incubation (as an indication of the ability to utilize carbohydrate) needs to be reconsidered.

The current classification of the genera *Bacteroides*, *Prevotella*, and *Porphyromonas* places emphasis on physiological characteristics (18). However, 16S rRNA sequence data have shown that *Porphyromonas asaccharolytica*, *Porphyromonas canoris*, *Porphyromonas circumdentaria*, *Porphyromonas endodontalis*, *Porphyromonas gingivalis*, *Porphyromonas salivosa*, and *B. levii* cluster together (2, 10). As three of these seven species are saccharolytic, it appears that the genus *Porphyromonas* should not be defined as consisting only of asaccharolytic organisms. Similarly, while the genus has been defined as consisting of species which fail to produce G6PDH and 6PGDH, *Porphyromonas canoris* and *Porphyromonas salivosa* produce both enzymes and thus do not conform completely to the current genus definition. These taxa are, however, deeply embedded in the *Porphyromonas* cluster (2, 10). A 16S rRNA sequence analysis of *Prevotella heparinolytica* and *Prevotella zoogleoformans* has shown that these species are most closely related to each other and related (albeit distantly) to members of the genus *Bacteroides* (2, 10). Paster et al. (10) proposed that *Prevotella heparinolytica* and *Prevotella zoogleoformans* belong to the *Bacteroides* cluster, which is consistent with our dehydrogenase and saccharolytic activity results. However, transfer of these species to the genus *Bacteroides* would require emendation of the current genus definition (both species fail to grow in the presence of bile and to date have been isolated only from oral cavities or individuals with oral diseases). It may be necessary to form a new genus to accommodate these species. 16S rRNA sequence data have revealed that the remaining *Prevotella* spp. which we studied (in which G6PDH and 6PGDH activities were not detected) grouped distinctly from the *Bacteroides* and *Porphyromonas* clusters but possessed some of the characteristics of both of these genera (i.e., they are saccharolytic but do not exhibit G6PDH and 6PGDH activities).

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