Reinstatement of Species Rank for *Bacteroides fragilis*, *B. ovatus*, *B. distasonis*, *B. thetaiotaomicron*, and *B. vulgatus*: Designation of Neotype Strains for *Bacteroides fragilis* (Veillon and Zuber) Castellani and Chalmers and *Bacteroides thetaiotaomicron* (Distaso) Castellani and Chalmers

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The organisms currently recognized as subspecies of *Bacteroides fragilis* have been shown to be genetically distinct. Species rank is therefore restored to these organisms, and type or neotype strains have been selected for the five species described. ATCC 25285 (= NCTC 9343) is designated the neotype strain of *Bacteroides fragilis* (Veillon and Zuber) Castellani and Chalmers; ATCC 29184 (= strain Werner E50 = NCTC 10582) is designated the neotype strain of *Bacteroides thetaiotaomicron* (Distaso) Castellani and Chalmers; ATCC 8503 is designated the type strain of *Bacteroides distasonis* Eggerth and Gagnon; ATCC 8483 is designated the type strain of *Bacteroides ovatus* Eggerth and Gagnon; and ATCC 8482 is designated the type strain of *Bacteroides vulgatus* Eggerth and Gagnon. Characteristics of these strains are presented.

Bacillus fragilis was first described by Veillon and Zuber in 1898 (19). Their description of this organism was meager, listing only morphological, colonial, and pathogenic characteristics: obligately anaerobic, gram-negative, nonsporeforming, nonmotile, somewhat pleomorphic rods with rounded ends, occurring singly or in pairs; subsurface colonies punctiform, circular or slightly irregular, convex, brownish yellow, semiopaque; surface colonies small, transparent, grayish; subcutaneous inoculations were pathogenic for guinea pigs or rabbits, causing abscesses and death after a week to a month; intravenous injections of live or killed cultures were toxic, causing death from cachexia.

In 1919, Castellani and Chalmers transferred the species to the genus *Bacteroides* as *Bacteroides fragilis* (4). They reported that colonies were neither pigmented nor fluorescent.

Eggerth and Gagnon in 1933 (7) published a detailed description of a new species, *Bacteroides convexus*, five strains of which had been isolated from human feces. In 1969, Werner (20) compared the reactions of 15 strains labeled *B. convexus* with those of 3 strains that had been deposited in the National Collection of Type Cultures (NCTC) as *B. fragilis*: NCTC 8560, 9343, and 9344. Characteristics of all strains were identical and, since the specific epithet *fragilis* had priority, Werner proposed that the name *B. convexus* be considered a nomen rejiciendum (20).

Holdeman and Moore (8) studied 326 strains of bacteria with characteristics that fit the minimal early descriptions of *B. fragilis* (4, 19). Clusters of strains within the group had phenotypic characteristics that were similar to those reported by Eggerth and Gagnon for *B. fragilis* (syn.: *B. convexus*), *B. thetaiotaomicron*, *B. distasonis*, *B. ovatus*, and *B. vulgatus* (7). However, many of the biochemical reactions of these strains were similar, and there appeared to be a continuum of variants without clear lines of demarcation (8). Variable characteristics included indole production and fermentation of particular carbohydrates. The guanine plus cytosine (G+C) content of the deoxyribonucleic acid (DNA) isolated from strains in each cluster was found to be similar, ranging from 40 to 44 mol%. Since the strains were morphologically and phenotypically quite similar, they were regarded as belonging to subspecies of *Bacteroides fragilis*, the type species of the genus *Bacteroides* (15).

Preliminary DNA homology studies, however, have shown that among these organisms there is a high level of diversity in the arrangement of the DNA nucleotides (11). These results are summarized in Table 1, which also includes the American Type Culture Collection (ATCC) numbers of the strains. When DNA preparations from organisms have this degree of diversity, they have usually been considered separate species (5, 16-18); indeed, many of the present species within the family *Enterobacte-*

Table 1. The interhomology of type or neotype strains of *B. fragilis*, *B. distasonis*, *B. vulgatus*, *B. thetaiotaomicron* and *B. ovatus*

Organisms as identified in reference 11	ATCC number	Interhomology of reference strains ^a				
		25285	8503	8482	29184	8483
<i>B. fragilis</i> subsp. <i>fragilis</i> (1) ^b	25285	100	5	10	21	15
<i>B. fragilis</i> subsp. <i>distasonis</i> (1)	8503	21	100	0	5	3
<i>B. fragilis</i> subsp. <i>vulgatus</i>	8482	24	9	100	9 ^c	8
<i>B. fragilis</i> subsp. <i>thetaitaomicron</i> (2)	29184	26	7	4	100	42
<i>B. fragilis</i> subsp. <i>ovatus</i> (1)	8483	23 ^c	4 ^c	8	39	100

^a The majority of the homology values are taken from reference 11.

^b Numbers in parentheses are from Table 5, reference 11. The numbers identify the homology group for which the strain was a reference organism.

^c Homology values determined in this study.

riaceae have much less DNA diversity than these organisms (2, 3). For example, strains of *Escherichia coli*, *Shigella boydii*, *Shigella dysenteriae*, *Shigella flexneri*, and *Shigella sonnei* all have greater than 80% DNA homology with *E. coli* K-12 (3). When duplex formation occurred at 60 C, the DNA homology of strains of *Salmonella typhi* ranged from 43 to 59% with *E. coli* (2).

Beerens et al. (1) found these strains to be serologically distinct. With agglutination tests, there were only very low levels of cross-reaction between some of the strains, and by the immunodiffusion technique there were no cross-reactions.

Therefore, in the interest of a more standardized concept of species, we propose the reinstatement of species rank for the various currently recognized subspecies of *B. fragilis*.

Werner (20) proposed that strain NCTC 9343 be designated the type (sic) strain of *B. fragilis*. This strain, isolated from an appendiceal abscess, was deposited in the NCTC in 1955 by L. P. Garrod. Since it is not one of the strains on which the original description of this organism by Veillon and Zuber was based, it cannot be considered the type strain (14). The Subcommittee on Gram-Negative Anaerobic Rods of the International Committee on Systematic Bacteriology has agreed to accept NCTC 9343 as the neotype strain of *B. fragilis* (10). Therefore, we propose that NCTC 9343 (= ATCC 25285) be designated the neotype strain of *Bacteroides fragilis* (Veillon and Zuber) Castellani and Chalmers.

Designation of the neotype strain is made here at the request of the International Subcommittee for Anaerobic Gram-Negative Rods to establish the proper taxonomic status for the species.

MATERIALS AND METHODS

Bacterial strains. *B. fragilis* ATCC 25285 (= NCTC 9343) was obtained from A. C. Sonnenwirth (Jewish Hospital, St. Louis, Mo.). *B. thetaiotaomicron* ATCC 29184 (= strain Werner E50 = NCTC 10582) was obtained from H. Werner (Hygiene-Institut der Universität, Bonn, Germany). *B. distasonis* ATCC 8503, *B. ovatus* ATCC 8483, and *B. vulgatus* ATCC 8482 were obtained from the ATCC.

Media and methods. Morphological and biochemical characteristics of these strains were determined with media and by methods described previously (9). All media were supplemented (per 100 ml) with 0.5 mg of hemin and 0.25 μ l of vitamin K₁.

Blood agar plates were prepared aerobically on the day of use from brain heart infusion agar, dehydrated base (BHIA, Difco), supplemented (per 100 ml) with 0.5 g of yeast extract, 0.5 mg of hemin, 0.25 μ l of vitamin K₁, and 5 ml of defibrinated sheep blood. Laked blood agar streak tubes were prepared anaerobically by adding sterile laked sheep blood to supplemented BHIA as described previously (9).

Fluorescence was investigated by transferring a strip of agar from a laked blood agar streak tube, as soon as colonies were apparent, to a sterile plate and surveying with a hand lens under ultraviolet light.

Methods for the isolation of DNA and for the determination of DNA homology values, using the membrane competition technique, were described elsewhere (12, 13).

RESULTS

The reactions and characteristics of ATCC 25285 after 5 days of incubation at 37 C, as well as those given in the description of *B. fragilis* (syn.: *B. convexus*) by Eggerth and Gagnon (7), are listed in Table 2.

A description of ATCC 25285 follows: Anaerobic, gram-negative, nonsporeforming, nonmotile rods. After incubation for 24 h in peptone-yeast extract-glucose broth (PYG), cells are 0.8 to 1.3 μ m in diameter by 1.6 to 8.0 μ m in

Table 2. Comparisons of the type and neotype strains of some *Bacteroides* species with their respective original species descriptions (Eggerth and Gagnon, ref. 7).

Reactions	<i>Bacteroides fragilis</i> (<i>B. convexus</i>)	ATCC 25285	<i>Bacteroides thetaiotaomicron</i>	ATCC 29184	<i>Bacteroides distasonis</i>	ATCC 8503	<i>Bacteroides ovatus</i>	ATCC 8483	<i>Bacteroides vulgatus</i>	ATCC 8482
Acid from	5 ^a		14		20		1		38	
Amygdalin	+	—+	+	+	+	w+	+	w+	—	—+
Arabinose	—	—	+	+	—	—w	—	+	+	+
Cellobiose	+	—w	+	w+	+	+w	+	+	—	—
Dextrin	+	+	+	+	+	+	+	+	+	+
Dulcitol	—	—	—	—	—	—	—	—	—	—
Erythritol	—	—	—	—	—	—	—	—	—	—
Esculin	+	w	+	w	+—	w	+	+	—+	—
Fructose	+	+	+	+	+	+w	+	+	+	+
Galactose	+	+	+	+	+	+	+	+	+	+
Glucose	+	+	+	+	+	+	+	+	+	+
Glycerol	—	—	—	—	—	—	—	—	—	—
Glycogen	+	+	+	+	—	—	+	+	+	+
Inositol	—	—	—	—	—	—	—	—	—	—
Inulin	+	+	+	+	+	+	+	+	+	+
Lactose	+	+	+	+	+	+	+	+	+	+
Maltose	+	+	+	+	+	+	+	+	+	+
Mannitol	—	—	—	—	—	—	—	+	—	—
Mannose	+	w+	+	+	+	+	+	+	+	+
Melezitose	—	—	+	+	+	w	—	+	—	—
Raffinose	+	+	+	+	+	+	+	+	+	+
Rhamnose	—	—	+	+	+	w	+	+	+	+
Salicin	—	—	+	—w	+	+	—	+	—	—
Sorbitol	—	—	—	—	—	—	—	—	—	—
Starch	+	+	+	+	+—	+	+	+	+	+
Sucrose	+	+	+	+	+	+	+	+	+	+
Trehalose	—	—	+	+	+	+	—	+	—	—
Xylose	+	+	+	+	+	+	+	+	+	+
Gas production	+	2	+—	2	—	—	+	—	+	+
Milk	c	c	c	c	c	c	c	c	c	c
Gelatin digestion	slow	w	—	—	—w	w	+	w	+	w
Indole production	—	—	+	+	—	—	+	+	—	—
H ₂ S production	+	+	+	+	+	w	+	w	+	+
Nitrate reduction	—	—	—	—	—	—	—	—	—	—

^aNumber of isolates on which the descriptions of Eggerth and Gagnon are based (7).

Symbols: +, positive reaction; + (carbohydrate culture), pH below 5.5; + (gelatin), medium does not solidify at 4 C; —, negative reaction; w, pH between 5.5 and 5.7; w (gelatin), liquefaction in less than half the time of control; c, curd; numbers (gas), amount estimated on '— to 4+' scale. Where two reactions are given (e.g. '—+'), the first was the more usual, the second observed less frequently.

length. Cells occur singly or in pairs and are straight or slightly curved, with rounded ends (Fig. 1). In carbohydrate media, vacuoles, which are typical of many strains of *B. fragilis*, are often seen.

Surface colonies on sheep-blood BHIA agar are punctiform, circular, entire, convex, grayish, semiopaque, and nonhemolytic. In laked blood agar streak tubes, surface colonies are translucent and buff colored. No fluorescence is observed under ultraviolet light on BHIA laked blood agar. Black pigment is not formed on laked blood BHIA streak tubes.

After incubation for 5 days in PYG, the pH of the medium was 5.4.

Eggerth and Gagnon reported (7) that their strains of *B. convexus* fermented both amygdalin and cellobiose. ATCC 25285 did not ferment either of these carbohydrates in 5 days but, after 3 weeks of incubation, both were weakly acid (pH 5.7 and 5.8, respectively, as compared with a pH of 6.2 in basal medium, peptone-yeast extract broth [PY]). Among other strains of *B. fragilis* that are in our collection, both of these reactions are variable; amygdalin is usually fermented and cellobiose is usually not. We have found for this group of organisms that the correlation between carbohydrate fermentation patterns and the homology groups is much better if fermentation tests are not considered positive unless the pH is 5.7 or below.

Although Veillon and Zuber stated that gelatin was not digested (19), Eggerth and Gagnon found gelatin to be liquefied after 20 to 30 days of incubation (7). This could have resulted from better growth conditions or from a longer holding period for cultures. ATCC 25285 weakly digested gelatin after 3 weeks of incubation (the chilled culture liquefied at room temperature in 23 min as compared with more than 60 min for an uninoculated control). Most of the strains of *B. fragilis* that we have examined do not liquefy gelatin, and the reaction is weak when it occurs.

Esculin and starch were hydrolyzed; resazurin and neutral red were reduced.

Addition of 20% bile to media was not inhibitory to growth.

Products of fermentation of PY and PYG are listed in Table 3. Propionate was not formed from lactate or threonine, but pyruvate was converted to acetate, propionate, and succinate.

The strain was resistant to penicillin but susceptible to chloramphenicol, clindamycin, erythromycin, and tetracycline when tested by the broth-disk method of Wilkins and Thiel (21).

The G+C content of the DNA is 42 mol%.

FIG. 1. *Bacteroides fragilis* ATCC 25285. Top, Cells from PY broth culture. Bottom, Cells from PY-glucose broth culture. See Fig. 5 for scale.

B. fragilis is widely recognized for its clinical significance and frequent occurrence in tissue infections.

A discussion of the other organisms previously (8, 15) accorded subspecies rank in the species *B. fragilis* follows.

Bacteroides thetaiotaomicron (Distaso) Castellani and Chalmers (*B. fragilis* subsp. *thetaitaomicron*).

B. thetaiotaomicron was first described by Distaso in 1912 (6) and was transferred to the genus *Bacteroides* by Castellani and Chalmers in 1919 (4). A more complete description of the organism was published in 1933 by Eggerth and Gagnon (7). Distaso's isolates, from normal human feces, were very pleomorphic gram-negative rods. The cells were elliptical, coccoid, or shaped like a kidney bean or a bell clapper. Some cells were uniformly stained, and some were stained only at the ends or with a transverse stripe. On blood agar plates, cells were 0.7 to 1.0 μ m in diameter by 1.0 to 2.0 μ m in length, usually occurring singly; in glucose broth, cells were often larger (up to 2.0 μ m in diameter and 4.0 μ m in length) and occurred in pairs (7).

Distaso reported that the cells of this organism were motile, but Eggerth and Gagnon believed what Distaso observed was only Brownian movement "which is very active" (7). None of their 14 strains was motile and none that we have examined was motile.

Colonies in carbohydrate agar deeps were transparent, moderately large, and circular with entire edges. Small amounts of gas were formed (6). On blood agar, colonies were 1.0 to 4.0 mm in diameter, peaked or convex, and grayish or yellowish, whereas surface colonies on glucose agar were 0.5 to 1.0 mm in diameter (7).

Table 3. Products of fermentation of type and neotype strains of some *Bacteroides* species

Acid product ^a	<i>B. fragilis</i> ATCC 25285		<i>B. thetaiotaomicron</i> ATCC 29184		<i>B. distasonis</i> ATCC 8503		<i>B. ovatus</i> ATCC 8483		<i>B. vulgatus</i> ATCC 8482	
	PY	PYG	PY	PYG	PY	PYG	PY	PYG	PY	PYG
Acetic acid	—	0.3–0.6 ^b	trace	0.8	—	0.3	trace	1.0	0.3	1.1
Propionic acid	1.4–1.6	0.2–0.4	1.5–2.5	trace	4.5	2.9	0.85	trace	5.2	trace
Isobutyric acid	—	—	trace	—	—	trace	trace	—	trace	—
Isovaleric acid	trace	—	trace	—	0.6	0.7	1.0	—	3.7	—
Lactic acid	—	—	—	—	0.35	6.9	—	—	0.5	0.25
Succinic acid	0.6–0.9	2.0–3.6	0.6–0.9	2.2–3.2	0.75	2.0	4.8	11.6	3.7	7.5

^aProducts were determined by gas-liquid chromatography after 5 days of incubation in peptone-yeast extract broth (PY) and peptone-yeast extract-glucose broth (PYG) (9).

^bMilliequivalents per 100 ml of culture.

Glucose and lactose were weakly fermented; milk was coagulated; gelatin was not digested; indole was formed (6).

In 1970, Werner deposited in the NCTC a strain with the above-mentioned characteristics. This strain of *B. thetaiotaomicron* (Werner E50 = NCTC 10582 = ATCC 29184) was isolated from human feces. It was used as the reference strain in a determination of DNA similarities (11), and it is here designated the neotype strain of *Bacteroides thetaiotaomicron* (Disaso) Castellani and Chalmers.

The interstrain DNA homology values (Table 1) show that *B. thetaiotaomicron* ATCC 29184 has 42% homology to *B. ovatus* ATCC 8483. Similar results were obtained in the reciprocal experiment (Table 1) and in the testing of additional strains from both species. Although they are still very distinct, *B. thetaiotaomicron* and *B. ovatus* appear to be more closely related to each other than to the other species under discussion.

The reactions of this strain and the characteristics of the species as given by Eggerth and Gagnon (7) are listed in Table 2.

A description of ATCC 29184 follows: Anaerobic, nonsporeforming, nonmotile, gram-negative rods. They are usually straight with rounded ends and occur singly or in pairs. In PYG, they are 0.9 to 1.9 μ m in diameter by 1.3 to 5.5 μ m in length, are quite pleomorphic, and often stain irregularly. In PY, they are smaller and are more homogeneous in size, shape, and staining (Fig. 2).

Surface colonies on sheep blood agar are punctiform, circular, entire, convex, semi-opaque, whitish, soft, and shiny. In laked blood agar streak tubes, colonies are buff colored and

FIG. 2. *Bacteroides thetaiotaomicron* ATCC 29184. Top, Cells from PY broth culture. Bottom, Cells from PY-glucose broth culture. See Fig. 5 for scale.

translucent and are neither fluorescent nor pigmented. Sheep blood is not hemolyzed.

Eggerth and Gagnon reported (7) that salicin was fermented by *B. thetaiotaomicron*. The strains of this species that we have studied vary in their ability to attack this substrate. The neotype strain did not ferment salicin even after 3 weeks of incubation, although there was good growth in the medium.

Addition of 20% bile to media did not inhibit growth.

The pH of PYG after 5 days of incubation was 5.3.

Esculin and starch were hydrolyzed; res-azurin, but not neutral red, was reduced.

Products of fermentation of PY and PYG are listed in Table 3. Propionate was not formed from lactate or threonine; pyruvate was converted to acetate and succinate.

Cells were resistant to penicillin but susceptible to chloramphenicol, clindamycin, erythromycin, and tetracycline.

The G+C content of the DNA is 42 mol%.

Bacteroides distasonis Eggerth and Gagnon (*B. fragilis* subsp. *distasonis*), *Bacteroides ovatus* Eggerth and Gagnon (*B. fragilis* subsp. *ovatus*), and *Bacteroides vulgatus* Eggerth and Gagnon (*B. fragilis* subsp. *vulgatus*).

Strains of *B. distasonis*, *B. ovatus*, and *B. vulgatus* were deposited in the ATCC by A. H. Eggerth, who first described these species (7). These strains have little DNA homology with each other or with strains of *B. fragilis* (11; Table 1). *B. ovatus* does have about 40% DNA homology with *B. thetaiotaomicron*. Since these strains were among those on which the original descriptions of these species were based, they are here designated the type strains of the species: *Bacteroides distasonis* Eggerth and Gagnon ATCC 8503, *Bacteroides ovatus* Eggerth and Gagnon ATCC 8483, and *Bacteroides vulgatus* Eggerth and Gagnon ATCC 8482.

Characteristics common to all three strains are as follows: Anaerobic, nonsporeforming, nonmotile, gram-negative rods; colonies on laked blood agar are neither pigmented nor fluorescent; growth is not inhibited by the addition of 20% bile; esculin and starch are hydrolyzed; and cells are resistant to penicillin but susceptible to chloramphenicol, clindamycin, erythromycin, and tetracycline.

The reactions of the type strains in pre-reduced media supplemented with vitamin K and heme (9) and the reactions reported by Eggerth and Gagnon for these species (7) are listed in Table 2.

Other characteristics, in good agreement with the original species descriptions, are presented below.

Bacteroides distasonis ATCC 8503.

In PYG, cells were 1.3 to 1.9 μm in diameter and 1.6 to 5.0 μm in length with rounded ends; they usually occurred singly, occasionally in pairs (Fig. 3).

Colonies on sheep-blood agar plates were pinpoint to 0.5 mm in diameter, circular, entire, convex, translucent to opaque, gray-white, soft, and smooth. Like some of the original strains, this strain was alpha-hemolytic.

The pH of PYG after 5 days of incubation was 5.4.

Characteristics of this strain which were not included in the original species description are as follows.

Resazurin, but not neutral red, was reduced.

Catalase was produced when this strain was

grown on PYG agar slants supplemented with vitamin K and heme, although it was not detected when the medium did not contain the supplements.

Products of fermentation of PY and PYG are listed in Table 3.

Propionate was not formed from lactate or threonine; neither pyruvate nor gluconate was converted to products other than those found after growth in PY.

The G+C content of the DNA is 44 mol%.

Bacteroides ovatus ATCC 8483.

In PYG, cells were 1.3 to 2.0 μm in diameter and 1.6 to 5.0 μm in length with rounded ends. Oval forms, which stain evenly, predominate. Cells usually occur singly, occasionally in pairs (Fig. 4).

Surface colonies on sheep blood agar were 0.5 to 1.0 mm in diameter, circular, entire, convex, pale buff colored, and semiopaque and had a slightly mottled appearance. Sheep blood was not hemolyzed.

FIG. 3. *Bacteroides distasonis* ATCC 8503. Top, Cells from PY broth culture. Bottom, Cells from PY-glucose broth culture. See Fig. 5 for scale.

FIG. 4. *Bacteroides ovatus* ATCC 8483. Top, Cells from PY broth culture. Bottom, Cells from PY-glucose broth culture. See Fig. 5 for scale.

FIG. 5. *Bacteroides vulgatus* ATCC 8482. Top, Cells from PY broth culture. Bottom, Cells from PY-glucose broth culture. Bar represents 10 μ m.

Resazurin and neutral red were reduced.

The pH of PYG after 5 days of incubation was 5.2.

The products of fermentation of PY and PYG are listed in Table 3.

Propionate was formed from lactate but not from threonine. Gluconate was not utilized, but pyruvate was converted to succinate, acetate, and propionate.

The G+C content of the DNA is 40 mol%.

Bacteroides vulgatus ATCC 8482.

In PYG, cells were 0.5 to 0.8 μ m in diameter and 1.5 to 7.7 μ m in length with rounded ends (Fig. 5). They may be quite pleomorphic with swellings or vacuoles. Cells usually occurred singly, but they may occur in pairs or short chains.

Surface colonies on blood agar were 1.0 to 2.0 mm in diameter, circular, entire, convex, grayish, semiopaque, and soft. Sheep blood was not hemolyzed.

Resazurin, but not neutral red, was reduced.

The products of fermentation of PY and PYG are listed in Table 3. Propionate was not formed from lactate or threonine. Neither pyruvate nor gluconate was utilized.

The G+C content of the DNA is 41 mol%.

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REPRINT REQUESTS

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LITERATURE CITED

- Beerens, H., P. Wattre, T. Shinjo, and C. Romond.

1971. Premiers resultats d'un essai de classification srologique de 131 souches de *Bacteroides* du groupe *fragilis* (Eggerthella). Ann. Inst. Pasteur Paris 121:187-198.
2. Brenner, D. J., and S. Falkow. 1971. Molecular relationships among members of the *Enterobacteriaceae*. Adv. Genet. 16:81-118.
3. Brenner, D. J., G. R. Fanning, F. J. Skerman, and S. Falkow. 1972. Polynucleotide sequence divergence among strains of *Escherichia coli* and closely related organisms. J. Bacteriol. 109:953-965.
4. Castellani, A., and A. J. Chalmers. 1919. Manual of tropical medicine, 3rd ed., p. 959-960. Williams Wood & Co., New York.
5. Dellaglio, F., V. Bottazzi, and L. D. Trovattelli. 1973. Deoxyribonucleic acid homology and base composition in some thermophilic lactobacilli. J. Gen. Microbiol. 74:289-297.
6. Distaso, A. 1912. Contribution a l'tude sur l'intoxication intestinale. Zentralbl. Bakteriol. Parasitenkd. Infektionskr. Hyg. Abt. 1 Orig. 62:433-468.
7. Eggerth, A. H., and B. H. Gagnon. 1933. The bacteroides of human feces. J. Bacteriol. 25:389-413.
8. Holdeman, L. V., and W. E. C. Moore. 1974. Genus I. *Bacteroides* Castellani and Chalmers 1919, p. 385-404. In R. E. Buchanan and N. E. Gibbons (ed.), Bergey's manual of determinative bacteriology, 8th ed. The Williams and Wilkins Co., Baltimore.
9. Holdeman, L. V., and W. E. C. Moore (ed.). 1975. Anaerobe laboratory manual, 3rd ed., p. 1-132. Virginia Polytechnic Institute and State University, Blacksburg.
10. International Committee on Nomenclature of Bacteria, Taxonomic Subcommittee for Gram-Negative Anaerobic Rods. 1970. Report. Int. J. Syst. Bacteriol. 20:297-300.
11. Johnson, J. L. 1973. Use of nucleic acid homologies in the taxonomy of anaerobic bacteria. Int. J. Syst. Bacteriol. 23:208-315.
12. Johnson, J. L., R. S. Anderson, and E. J. Ordal. 1970. Nucleic acid homologies among oxidase-negative *Moraxella* species. J. Bacteriol. 101:568-573.
13. Johnson, J. L., and C. S. Cummins. 1972. Cell wall composition and deoxyribonucleic acid similarities among the anaerobic coryneforms, classical propionibacteria, and strains of *Arachnia propionica*. J. Bacteriol. 109:1047-1066.
14. Lapage, S. P., P. H. A. Sneath, E. F. Lessel, V. B. D. Skerman, H. P. R. Seeliger, and W. A. Clark (ed.). 1975. International code of nomenclature of bacteria, 1976 revision. American Society for Microbiology, Washington, D.C.
15. Moore, W. E. C., and L. V. Holdeman. 1973. New names and combinations in the genera *Bacteroides* Castellani and Chalmers, *Fusobacterium* Knorr, *Eubacterium* Prvot, *Propionibacterium* Delwiche, and *Lactobacillus* Orla-Jensen. Int. J. Syst. Bacteriol. 23:69-74.
16. Palleroni, N. J., R. Kunisawa, R. Contopoulou, and M. Doudoroff. 1973. Nucleic acid homologies in the genus *Pseudomonas*. Int. J. Syst. Bacteriol. 23:333-339.
17. Scardovi, V., and F. Crociani. 1974. *Bifidobacterium catenulatum*, *Bifidobacterium dentium*, and *Bifidobacterium angulatum*: three new species and their deoxyribonucleic acid homology relationships. Int. J. Syst. Bacteriol. 24:6-20.
18. Trovattelli, L. D., F. Crociani, M. Pedinotti, and V. Scardovi. 1974. *Bifidobacterium pullorum* sp. nov.: a new species isolated from chicken feces and a related group of bifidobacteria isolated from rabbit feces. Arch. Microbiol. 98:187-198.
19. Veillon, A., and A. Zuber. 1898. Recherches sur quelques microbes strictement anarobies et leur role en

- pathologie. Arch. Med. Exp. Anat. Pathol. 10:517-545.
20. Werner, H. 1969. *Bacteroides convexus* Eggerth und Gagnon 1933 identisch mit *Bacteroides fragilis* (Veillon und Zuber 1898) Castellani und Chalmers 1919. Zentralbl. Bakteriol. Parasitenkd. Infektionskr. Hyg. Abt. 1 Orig. 211:344-353.
21. Wilkins, T. D., and T. Thiel. 1973. A modified broth-disk method for testing the antibiotic susceptibility of anaerobic bacteria. Antimicrob. Agents Chemother. 3:350-356.