Transfer of *Pimelobacter tumescens* to *Terrabacter* gen. nov. as *Terrabacter tumescens* comb. nov. and of *Pimelobacter jensenii* to *Nocardioides* as *Nocardioides jensenii* comb. nov.

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The phylogenetic interrelationship of members of the genera *Nocardioides* and *Pimelobacter* were examined by using reverse transcriptase sequencing of 16S ribosomal ribonucleic acid. The sequence studies demonstrated that *Nocardioides albus*, *Nocardioides luteus*, *Pimelobacter jensenii*, and *Pimelobacter simplex* represent a coherent phylogenetic group at the genus level, whereas *Pimelobacter tumescens* occupies a separate line of descent. On the basis of sequence data and the chemotaxonomic distinctiveness of the latter organism, we propose that *Pimelobacter tumescens* be reclassified in a new genus, *Terrabacter*, as *Terrabacter tumescens* comb. nov.

Arthrobacter simplex and *Arthrobacter tumescens* are among the few named species of coryneform bacteria which contain cell wall peptidoglycans based on LL-2,6-diaminopimelic acid (5, 16). The two species thus differ in peptidoglycan composition from *Arthrobacter globiformis*, the type species of the genus, which contains lysine as the dibasic amino acid (16). Although there is now general agreement that these species should be removed from the genus *Arthrobacter*, their taxonomic position remains controversial (10). Suzuki and Komagata (19) proposed the creation of a new genus, *Pimelobacter*, to accommodate these species. A third species, *Pimelobacter jensenii*, was also proposed for an atypical *A. simplex* strain (19). However, there is evidence of considerable chemical heterogeneity within the genus *Pimelobacter* (3, 12, 19). *Pimelobacter* (*Arthrobacter*) *simplex* and *P. jensenii* are unusual among coryneform and related bacteria in producing complex mixtures of straight-chain saturated, monounsaturated, and iso-, anteiso-, and 10-methyl branched fatty acids (3, 12, 19-21). However, *Pimelobacter tumescens* differs from these species in lacking 10-methyl branched acids and in containing substantial levels (ca. 20%) of monounsaturated terminally branched acids (3). *P. simplex* and *P. jensenii* also differ from *P. tumescens* in synthesizing 2-hydroxylated long-chain fatty acids (3, 12). The polar lipid compositions of these taxa are also quite different. *P. simplex* and *P. jensenii* possess diphosphatidylglycerol, phosphatidylglycerol, and hydroxyphosphatidylglycerol (3, 12, 21). However, *P. tumescens* lacks hydroxyphosphatidylglycerol and in addition synthesizes two unknown aminophosphoglycolipids (3, 12). Such major differences in lipid composition between *P. simplex* and *P. jensenii* on the one hand and *P. tumescens* on the other hand indicate that these taxa should probably not be accommodated in the same genus. Interestingly, the lipid composition of *P. simplex* and *P. jensenii* is indistinguishable from that of members of the genus *Nocardioides* (3, 12). Indeed, primarily on the basis of similarity in lipid composition, O'Donnell et al. (12) proposed that *P. simplex* be transferred to the genus *Nocardioides*. However, *P. simplex* does not possess a nocardioform morphology (extended primary and aerial

mycelium), and its placement within the genus *Nocardioides* has been questioned (14).

16S ribosomal ribonucleic acid (rRNA) cataloging shows that *P. simplex* is well removed from the arthrobacters sensu stricto and indicates that this species occupies a line of descent the branching point of which is as low as that of other major lines within the actinomycetes (18, 19). To date comparative sequencing studies with other members of *Pimelobacter* and *Nocardioides* have not been made. Therefore, in an attempt to clarify the relationship of *P. simplex* to the genus *Nocardioides* and to resolve the position of *P. tumescens*, we analyzed and compared long stretches of the 16S rRNA primary structures of these taxa.

MATERIALS AND METHODS

Cultures and cultivation. Type strains *Nocardioides albus* DSM 43109, *Nocardioides luteus* NCIB 11455, *P. jensenii* DSM 20641, *P. simplex* NCIB 8929, and *P. tumescens* NCIB 8914 were grown in shake flasks (casein peptone, 10 g; yeast extract, 5 g; glucose, 5 g; NaCl, 5 g; water, 1 liter; pH 7.4) to late exponential phase at 25°C.

Sequence determination and analysis. Crude ribonucleic acid was isolated as described previously (7). Reverse transcriptase sequencing of ribonucleic acid was achieved by using the method of Lane et al. (11). The sequence of oligonucleotide primers, their target sites, and the electrophoretic separation conditions used for complementary deoxyribonucleic acid have been described by Embley et al. (7). Some sequence ambiguities were resolved by using terminal transferase (6). Sequence data were aligned and homology values were determined with the Beckman Microgenie program (15). Calculation of evolutionary distance values (K_{nuc}) and construction of phylogenetic trees followed previously published procedures (8, 9).

RESULTS AND DISCUSSION

The partial reverse transcriptase sequences of the five strains investigated are shown aligned in Fig. 1. The homology and derived K_{nuc} values from 1,449 bases used for determining intragroup relationships are shown in Tables 1

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[illegible]

and 2. The phylogenetic tree derived from the latter values is depicted in Fig. 2. The two *Nocardioides* species which we examined possess very high sequence homology (>98%). *P. simplex* and *P. jensenii* also share a relatively high level of homology (ca. 95%) and are approximately equidistant from each other and *Nocardioides* species. *P. tumescens* displays significantly lower levels of homology to these species (ca. 90%). To ascertain the intergroup relationships, the sequences of the species described above were compared with those of 18 previously studied actinomycetes from 14 genera (2, 4, 7; E. Stackebrandt, J. Smida, and M. D. Collins, J. Gen. Appl. Microbiol., in press; J. Smida, T. M. Embley, M. D. Collins, D. Hahn, and E. Stackebrandt, unpublished data). The latter comparison was based on 480 nucleotides involving only variable positions between points 200 and 1,435 (*Escherichia coli* numbering system [1]). Representative homology values are shown in Table 1. The branching pattern (Fig. 3) indicates that all *Nocardioides* spp. and pimelobacters constitute a separate line of descent, comparable in phylogenetic depth to the depths of the major

lines (i.e., *Streptovorticillium*, *Frankia*, *Actinomyces*, *Propionibacterium*, *Pseudonocardia*, *Bifidobacterium*, and mycolic acid-containing taxa). It is evident from both trees that *P. tumescens* is only loosely related to *P. simplex*, *P. jensenii*, *N. albus*, and *N. luteus*, forming an individual subline.

The high levels of sequence homology among *N. albus*, *N. luteus*, *P. jensenii*, and *P. simplex* are in accordance with the high degree of chemical similarity among these species (3, 12) and the results of phage typing (13). These data strongly support the union of *Nocardioides* and *Pimelobacter* into a single genus, for which *Nocardioides* has priority (by date of publication). The inclusion of *P. simplex* and *P. jensenii* in the genus *Nocardioides* makes the latter heterogeneous with respect to morphology. However, there is now evidence that morphological characters are not reliable indicators of relatedness (17, 18). The degree of morphological differences among these taxa is in any case debatable. Prauser (13) noted that strain IMET 7801, initially intended to be the type strain of *N. albus*, lost the ability to form aerial mycelium on

Nal CC6CCU6666AGUAC66CC6CAAG6CUAAACUCAAAG6AAU6AC66666CC6CACAA6C66C66AGCAUGC66AUAAUUC6AUnAAC6C6A6AACC UUACC U666UU6ACAU
 Nlu CC6CCU6666AGUAC66CC6CAAG6CUAAACUCAAAG6AAU6AC66666CC6CACAA6C66C66AGCAUGC66AUAAUUC6AUnAAC6C6A6AACC UUACC U666UU6ACAU
 Psi CC6CCU6666AGUAC66CC6CAAG6CUAAACUCAAAG6AAU6AC66666CC6CACAA6C66C66AGCAUGC66AUAAUUC6AUnAAC6C6A6AACC UUACC U666UU6ACAU
 Pje CC6CCU6666AGUAC66CC6CAAG6CUAAACUCAAAG6AAU6AC66666CC6CACAA6C66C66AGCAUGC66AUAAUUC6AUnAAC6C6A6AACC UUACC U666UU6ACAU
 Ptu CC6CCU6666AGUAC66CC6CAAG6CUAAACUCAAAG6AAU6AC66666CC6CACAA6C66C66AGCAUGC66AUAAUUC6AUnAAC6C6A6AACC UUACC U666UU6ACAU

 Nal CACC66AAG6CUAGAGAUAC66CCCUUUUAGUC 666UACAG66U66U6CAU66CUG6CAGCUC6UG6CUG6AGAU6U666UAA6UCC6CAAC6AG6C6CAACCCU6CUC
 Nlu CACC66AAG6CUAGAGAUAC66CCCUUUUAGUC 666UACAG66U66U6CAU66CUG6CAGCUC6UG6CUG6AGAU6U666UAA6UCC6CAAC6AG6C6CAACCCU6CUC
 Psi CACC66AAG6CCCUAGAGAUAG666nCUUUUAGAUACU66U6UACAG66U66nCAU66CUG6CAGCUC6UG6CUG6AGAU6U666UAA6UCC6CAAC6AG6C6CAACCCU6CUC
 Pje U66C66AAG6CUUAGAGAUAG66CCCUUUUAGUC 666UACAG66U66U6CAU66CUG6CAGCUC6UG6CUG6AGAU6U666UAA6UCC6CAAC6AG6C6CAACCCU6CUC
 Ptu CACC66AUCACUAGAGAU 666U6nCUUUC66CUG6U6UACAG66U66U6CAU66U6nCUUUC6CAGCUC6UG6CUG6AGAU6U666UAA6UCC6CAAC6AG6C6CAACCCU6CUC

 Nal UAU6UUGCCAGCAUUC66U U6666ACUUAAGAGAGU66C6666U6nAACU66AG6A66U6666U6AGC6U6nAA6U6CAU66CCCUUUAU6U6CAG666CUUAC6CAU6CUACAA
 Nlu UAU6UUGCCAGCAUUC66U U6666ACUUAAGAGAGU66C6666U6nAACU66AG6A66U6666U6AGC6U6nAA6U6CAU66CCCUUUAU6U6CAG666CUUAC6CAU6CUACAA
 Psi CAU6UUGCCAGC666UUAU6CC6666ACUUAAGAGAGU66C6666U6nAACU66AG6A66U6666U6AGC6U6nAA6U6CAU66CCCUUUAU6U6CAG666CUUAC6CAU6CUACAA
 Pje UAU6UUGCCAGCAGUAAU66U6666ACUUAAGAGAGU66C6666U6nAACU66AG6A66U6666U6AGC6U6nAA6U6CAU66CCCUUUAU6U6CAG666CUUAC6CAU6CUACAA
 Ptu UAU6UUGCCAGCAGU66U6666ACU6nU66AGAGU66C6666U6nAACU66AG6A66U6666U6AGC6U6nAA6U6CAU66CCCUUUAU6U6CAG666CUUAC6CAU6CUACAA

 Nal U66CC66UACnAA666CU6C6AUCC6U6nAA666U6AG6CAUCCAAAAAGCC66UCU6AU6C66AUU6666U6C6AACUC6ACCCCAUGA6U6C66AGUC6CU6AUAU6C6A6U6C
 Nlu U66CC66UACnAA666CU6C6AUCC6U6nAA666U6AG6CAUCCAAAAAGCC66UCU6AU6C66AUU6666U6C6AACUC6ACCCCAUGA6U6C66AGUC6CU6AUAU6C6A6U6C
 Psi U66CC66UACnAA666CU6C6AUCC6U6nAA666U6AG6CAUCCAAAAAGCC66UCU6AU6C66AUU6666U6C6AACUC6ACCCCAUGA6U6C66AGUC6CU6AUAU6C6A6U6C
 Pje U66CC66UACnAA666CU6C6AUCC6U6nAA666U6AG6CAUCCAAAAAGCC66UCU6AU6C66AUU6666U6C6AACUC6ACCCCAUGA6U6C66AGUC6CU6AUAU6C6A6U6C
 Ptu U66CC66UACnAA666CU6C6AUCC6U6nAA666U6AG6CAUCCAAAAAGCC66UCU6AU6C66AUU6666U6C6AACUC6ACCCCAUGA6U6C66AGUC6CU6AUAU6C6A6U6C

 Nal AGCAAC6CUG666U6AAUAC6U6CC666CUU6UACACACCC66n6CUGAC6CAGCAGAAACU66CAACACCC6AAGCCAGU66CCCAACUC6UAA66A666A6CUG6CA66U666
 Nlu AGCAAC6CUG666U6AAUAC6U6CC666CUU6UACACACCC66n6CUGAC6CAGCAGAAACU66CAACACCC6AAGCCAGU66CCCAACUC6UAA66A666A6CUG6CA66U666
 Psi AGCAAC6CUG666U6AAUAC6U6CC666CUU6UACACACCC66C6CUGAC6CAGCAGAAACU66CAACACCC6AAGCCAGU66CCCAACUC6UAA66A666A6CUG6CA66U666
 Pje AGCAAC6CUG666U6AAUAC6U6CC666CUU6UACACACCC66C6CUGAC6CAGCAGAAACU66CAACACCC6AAGCCAGU66CCCAACUC6UAA66A666A6CUG6CA66U666
 Ptu AGCAAC6CUG666U6AAUAC6U6CC666CUU6UACACACCC66C6CUGAC6CAGCAGAAACU66CAACACCC6AAGCCAGU66CCCAACUC6UAA66A666A6CUG6CA66U666

Nal 6CU66C6AU
 Nlu 6CU66C6AU
 Psi 6CU66C6AU
 Pje 6CU66C6AU
 Ptu 6CU66C6AU

FIG. 1. Partial 16S rRNA sequences of *N. albus* (Nal), *N. luteus* (Nlu), *P. jensenii* (Pje), *P. simplex* (Psi), and *P. tumescens* (Ptu). The dots indicate an unsequenced region of 18 nucleotides. n, Undetermined nucleotide. A space indicates a nucleotide gap. The asterisk at the 5' terminus corresponds to position 1, and the last base at the 3' terminus corresponds to position 1,497 of the *E. coli* sequence (1).

continued subculture. Furthermore, *Nocardioides* species exhibit a developmental cycle in which with increasing age the substrate mycelium fragments into irregular rod-shaped to coccoid elements, giving the appearance of coryneform morphology. Therefore, we consider the morphological objections insufficient grounds for retaining the separateness of these genera. We concur with the proposal of O'Donnell et al. (12) to reclassify *P. simplex* as *Nocardioides simplex* and also propose the new combination *Nocardioides jensenii*. The ribonucleic acid studies do not support the suggestion of Suzuki and Komagata (19) that *P. tumescens*, *P. simplex*, and *P. jensenii* should be included in the same genus. *P.*

tumescens has been shown to be quite different from the latter two species (3). In view of the isolated phylogenetic position of *P. tumescens*, together with its chemical distinctiveness, we suggest that this organism be reclassified in a new genus, *Terrabacter*, as *Terrabacter tumescens* comb. nov.

Description of *Nocardioides jensenii* (Suzuki and Komagata) comb. nov. The description below is based on data from references 3 and 17. A rod-coccus growth cycle occurs during growth on complex media. Exponential-phase cells are long, irregular rods (ca. 0.6 to 1.0 by 2.0 to 7.0 μ m). Older cultures are composed of coccoid cells. Aerial myce-

TABLE 1. K_{nuc} values for *Nocardioides* and *Pimelobacter* species

Strain ^a	K_{nuc} value with: ^b			
	<i>Pimelobacter jensenii</i> DSM 29641 ^T	<i>Pimelobacter tumescens</i> NCIB 8914 ^T	<i>Nocardioides albus</i> DSM 43109 ^T	<i>Nocardioides luteus</i> NCIB 11455 ^T
<i>Pimelobacter simplex</i> NCIB 8929 ^T	0.122 (0.091)	0.214 (0.101)	0.112 (0.059)	0.107 (0.058)
<i>Pimelobacter jensenii</i> DSM 29641 ^T		0.201 (0.087)	0.093 (0.057)	0.117 (0.054)
<i>Pimelobacter tumescens</i> NCIB 8914 ^T			0.230 (0.109)	0.231 (0.101)
<i>Nocardioides albus</i> DSM 43109 ^T				0.019 (0.015)

^a NCIB, National Collection of Industrial Bacteria; DSM, Deutsche Sammlung von Mikroorganismen.

^b The values not in parentheses were calculated from 480 nucleotides. The values in parentheses were based on a comparison of 1,449 nucleotides.

FIG. 2. Unrooted phylogenetic tree displaying the interrelationship of *Nocardioideae* and *Pimelobacter* species. The branching pattern was derived from K_{nuc} values (Table 1). Bar = 0.01 K_{nuc} unit.

lium is not formed. Nonmotile. Colonies are glossy, smooth, entire, and white. Growth in 5% NaCl but not 10% NaCl. Does not grow at 37°C. Catalase positive. Oxidase negative. Nutritionally nonexacting; growth occurs in suitable mineral salts medium with an ammonium salt or nitrate as the sole nitrogen source and glucose as the carbon-plus-energy source. Acid is not produced from glucose and other sugars in peptone-based media. A wide range of organic compounds are utilized as sole or principal carbon-plus-energy sources for growth, including glucose, sucrose, L-rhamnose, and acetate. Deoxyribonuclease is produced. Urease positive. Nitrate is reduced to nitrite. The cell wall peptidoglycan is based on LL-2,6-diaminopimelic acid (type LL-A₂pm-Gly₃). The nonhydroxylated long-chain fatty acids are complex, consisting of straight-chain saturated, monounsaturated, and

iso-, anteiso-, and 10-methyl-branched types; 2-hydroxy fatty acids are also produced. The polar lipids comprise diphosphatidylglycerol, phosphatidylglycerol, phosphatidylinositol, and hydroxyphosphatidylglycerol. The major isoprenoid quinone is MK-8 (II,III-H₄). The guanine-plus-cytosine content of the deoxyribonucleic acid is 68.8 mol% (thermal denaturation method).

The type strain is strain NCIB 9770 (= JCM 1364 = DSM 20641). The description of the type strain corresponds to that of the species.

Description of *Terrabacter* gen. nov. *Terrabacter* (Ter.ra. bac'ter. L. n. terra, earth; M. L. masc. n. bacter, masc. equivalent of Gr. neut. n. bacterum, a rod; *Terrabacter*, earth [soil] rod). The description below is based on data from references 3, 8, 10, and 17. A rod-coccus growth cycle occurs during growth in complex media. Irregular rods are observed in exponential-phase cultures; stationary-phase cultures are composed of mainly coccoid cells. Both rods and coccoid forms are gram positive. Cells are non-acid fast and do not form endospores. Rods are nonmotile or occasionally motile. Growth at 10 and 35°C. Optimum temperature for growth, ca. 25 to 30°C. Does not survive heating at 63°C for 30 min. Growth in 5% NaCl. Catalase positive. Oxidase negative. Obligately aerobic. Acid is not produced from glucose and other sugars in peptone-based media. Cellulose is not hydrolyzed. Nitrate is reduced to nitrite. The cell wall peptidoglycan contains LL-2,6-diaminopimelic acid (variation A3γ) as the diamino acid. Mycolic acids are absent. The long-chain cellular fatty acids are primarily of the iso-methyl branched types; straight-chain saturated, anteiso-methyl branched, and monounsaturated iso-methyl branched acids are also present. The polar lipids comprise diphosphatidylglycerol, phosphatidylethanolamine, phosphatidylinositol, and some unknown amino-containing phospho-

FIG. 3. Unrooted phylogenetic tree displaying the relationship of *Nocardioideae* and *Pimelobacter* species to other reference actinomycetes. Bar = 0.04 K_{nuc} unit.

TABLE 2. 16S rRNA sequence homologies for *Nocardioides* species, *Pimelobacter* species, and some reference actinomycetes

Strain ^a	% Homology with ^b :													
	<i>Pimelobacter simplex</i> NCIB 8929 ^T	<i>Pimelobacter jensenii</i> DSM 29641 ^T	<i>Pimelobacter tumescens</i> NCIB 8914 ^T	<i>Nocardioides albus</i> DSM 43109 ^T	<i>Nocardioides luteus</i> NCIB 11455 ^T	<i>Bifidobacterium bifidum</i> DSM 20456 ^T	<i>Streptovorticillium baldacii</i> DSM 40845 ^T	<i>Propionibacterium freudenreichii</i> DSM 20271 ^T	<i>Actinomyces bovis</i> DSM 43014 ^T	<i>Frankia</i> sp. strain Ag45/Mut15	<i>Mycobacterium tuberculosis</i> H37/RV	<i>Nocardia asteroides</i> DSM 43005	<i>Tsukamurella paurometabolum</i> DSM 20162 ^T	<i>Rhodococcus erythropolis</i> DSM 43188
<i>Pimelobacter jensenii</i> DSM 29641 ^T	88.7 (94.2)													
<i>Pimelobacter tumescens</i> NCIB 8914 ^T	81.4 (90.6)	82.4 (91.8)												
<i>Nocardioides albus</i> DSM 43109 ^T	89.6 (94.4)	90.7 (94.5)	80.2 (89.9)											
<i>Nocardioides luteus</i> NCIB 11455 ^T	90.0 (94.5)	89.2 (94.8)	80.1 (90.6)	98.1 (98.5)										
<i>Bifidobacterium bifidum</i> DSM 20456 ^T	62.2	64.7	65.2	63.8	63.4									
<i>Streptovorticillium baldacii</i> DSM 40845 ^T	73.6	77.0	77.4	74.5	75.0	63.0								
<i>Propionibacterium freudenreichii</i> DSM 20271 ^T	78.8	74.6	75.4	73.5	76.3	63.1	71.3							
<i>Actinomyces bovis</i> DSM 43014 ^T	71.5	69.1	74.5	68.2	70.3	67.7	69.7	69.0						
<i>Frankia</i> sp. strain Ag45/Mut15	76.6	76.6	77.6	74.2	75.5	59.0	74.3	70.7	69.0					
<i>Mycobacterium tuberculosis</i> H37/RV	78.2	77.0	77.0	74.2	75.7	62.2	71.4	75.8	72.4	73.6				
<i>Nocardia asteroides</i> DSM 43005	76.8	77.8	78.0	76.2	77.1	62.3	75.0	73.5	70.1	76.9	81.6			
<i>Tsukamurella paurometabolum</i> DSM 20162 ^T	79.6	76.7	80.8	75.5	76.8	63.5	75.4	76.7	73.8	77.0	83.5	84.0		
<i>Rhodococcus erythropolis</i> DSM 43188	80.1	79.4	80.0	78.7	79.8	63.9	76.2	76.3	72.3	78.3	82.3	88.0	87.7	
<i>Saccharomonospora viridis</i> ATCC 15386 ^T	74.7	73.0	71.9	72.3	70.9	59.0	71.4	70.8	69.9	71.9	77.4	77.1	77.3	78.7

^a ATCC, American Type Culture Collection; DSM, Deutsche Sammlung von Mikroorganismen; NCIB, National Collection of Industrial Bacteria.^b The values in parentheses for *Nocardioides* and *Pimelobacter* species were based on a comparison of 1,449 nucleotides. The values not in parentheses were calculated from 480 nucleotides.

glycolipids. The major isoprenoid quinones are tetrahydrogenated menaquinones with eight isoprene units [MK-8 (II,III-H₄)]. The guanine-plus-cytosine content of the deoxyribonucleic acid is 69.8 to 73.4 mol% (thermal denaturation method). Phylogenetically, *Terrabacter* belongs to the actinomycetes subdivision, forming together with *Nocardioidea* a separate line of descent. The type species is *Terrabacter tumescens*.

Description of *Terrabacter tumescens* (Jensen) comb. nov. The description below is based on data from references 3, 8, 10, and 17. In addition to the characteristics of the genus, the salient characteristics are given below. A rod-coccus cycle occurs during growth on complex media. Cells from older cultures are coccoid (diameter, 0.5 to 0.8 µm). After transfer to fresh complex media long, irregular rods (0.6 to 1.2 by 2.0 to 6.0 µm) are formed. The long rods show primary branching. Aerial mycelium is not formed. Generally nonmotile (occasionally motile strains occur). Colonies are glossy, entire, smooth, and gray or white. Growth at 10 and 35°C; may or may not grow at 37°C. Optimum temperature for growth ca. 25 to 30°C. Most strains grow in 5% NaCl. Obligately aerobic. Acid is not formed from glucose and other sugars in peptone-based media. Thiamine is the only growth factor required (when thiamine is provided, the organism utilizes an ammonium salt or nitrate as the sole nitrogen source in mineral salts medium with glucose as the carbon-plus-energy source). A wide range of organic compounds is utilized as sole or principal carbon-plus-energy sources for growth, including acetate, D-alanine, crotonate, inositol, α-D-glucosamine, D-mannose, and raffinose; D-glucuronate, L-ornithine, D-phenylalanine, and uric acid are not utilized. Gelatin, hippurate, and tyrosine are hydrolyzed. Starch may or may not be hydrolyzed. Some strains hydrolyze Tween 80. Deoxyribonuclease is produced. Urease and sulfatase negative. Some strains produce H₂S. The guanine-plus-cytosine content of the deoxyribonucleic acid is 69.8 to 72.4 mol% (thermal denaturation method). Occurs in soil.

The type strain is strain NCIB 8914 (= DSM 20308 = ATCC 6947). In most respects the description of the type strain corresponds to that of the species. The type strain is nonmotile. Starch and Tween 80 are hydrolyzed. H₂S is not produced.

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