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# PROPOSAL TO REJECT THE GENUS HYDROGENOMONAS: TAXONOMIC IMPLICATIONS

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ABSTRACT. Fifty-six strains of "hydrogen bacteria" and related nonautotrophic bacteria, including nearly all existing named Hydrogenomonas spp., have been compared. It is proposed that the genus Hydrogenomonas should be rejected, since its type species H. pantotropha, appears to be a nomen dubium; and that the various species of "hydrogen bacteria" should be assigned to other genera, not specifically characterized by the ability to grow autotrophically with $H_2$.

The two species of hydrogen bacteria most frequently isolated by enrichment show a peritrichous or degenerate peritrichous flagellar arrangement; one is nonpigmented, the other produces yellow (carotenoid) cellular pigments. Of the various possible generic assignments for these two species, assignment to the genus Alcaligenes is proposed. The nonpigmented species, previously named Hydrogenomonas eutropha, but never legitimately described, is here described as A. eutrophus. The yellow species which includes both facultatively autotrophic and nonautotrophic strains, is described as a new species, A. paradoxus. The Gram-negative, coccoid hydrogen bacterium, formerly known as Micrococcus denitrificans, is placed in a new

genus, Paracoccus. The polarly flagellated species of hydrogen bacteria, including the previously named species Hydrogenomonas facilis, H. flava, H. ruhlandii and Pseudomonas saccharophila, are all assigned to the genus Pseudomonas.

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Defined as a physiological group, the "hydrogen bacteria" are aerobic chemolithotrophs that can use the oxidation of molecular hydrogen as an energy source. In 1909, Orla-Jensen proposed the genus Hydrogenomonas to accommodate these organisms. At that time, the only named species (and hence the type species of the new genus) was Bacillus pantotrophus. This species had been described by Kaserer (1906) as a Gram-negative polarly flagellated rod; it was further characterized by the production of a yellow cellular pigment, and by the ability to grow heterotrophically with a variety of organic substrates. The genus Hydrogenomonas accordingly became a repository for aerobic bacteria which resemble in their morphology and in many physiolotical respects members of the genus Pseudomonas, but which are distinguished by their ability to grow autotrophically with hydrogen. Several other monotypic species were added by later workers (Niklewski 1910; Schatz and Bovell 1952; Packer and Vishniac 1955; Kistner 1953; Eberhardt 1965).

From the accompanying discussion in Orla-Jensen's paper, it is evident that his proposal of the genus was predicated on the assumption that growth at the expense of $H_2$ oxidation is a highly significant physiological and ecological property, which defines a small and specialized group of aerobic bacteria. Later work, however, indicates that his assumption is probably incorrect. In the first place, all described "hydrogen bacteria" have proved to be nutritionally versatile chemoorganotrophs. This raises the question, so far never systematically examined, of their possible taxonomic relationships to strictly chemoorganotrophic bacteria. In the second place, it has been reported that some hydrogen bacteria may lose their ability to grow autotrophically after growth on organic media (Kluyver and Manten 1942; Packer and Vishniac 1955); such cultures have, of course, lost the defining character of the genus. Lastly, it has become evident that organisms which are hydrogen bacteria by physiological definition may occur in several different structural groups of unicellular eubacteria; they include

one Gram-negative immotile coccus, Micrococcus denitrificans (Beijerinck and Minkman 1910; Verhoeven, Koster and Van Nievelt 1954; Vogt 1965) as well as Gram-positive organisms assignable to the Mycobacterium-Nocardia complex, Streptomyces and Streptosporangium (Hirsch 1961).

One further problem concerns the type species. Kaserer's description of B. pantotrophus is inadequate, and no authentic strains exist. The maintenance of the genus accordingly depends on the reisolation of a hydrogen bacterium which corresponds sufficiently closely to the published descriptions of the type species to be acceptable as a neotype.

In the past few years, we have assembled a large collection of strains of Gram-negative hydrogen bacteria. It includes most of the surviving named strains, as well as many strains that we have isolated from soil and water by appropriate enrichment procedures. (One supposedly authentic named strain of H. carboxydovorans Kistner (1953) received by us did not in any way resemble its description and was eliminated from our studies). This collection has been subjected to taxonomic analysis, using the methodology previously developed by us for the characterization of aerobic pseudomonads (Stanier et al. 1966). A total of 160 phenotypic characters was determined for each strain. We have also included in this study certain strains of nonautotrophic Gram-negative bacteria which appeared to resemble hydrogen bacteria in certain phenotypic respects. The collection could be subdivided into six primary groups, the principal distinguishing attributes of which are shown in Tables 1 and 2. The flagellar arrangement of representative strains of each group is shown in Table 3.

Group A comprises the type and one other strain of Micrococcus denitrificans. This Gram-negative immotile coccus obviously should not be placed in the same genus as the motile, rod-shaped Gram-negative hydrogen bacteria; and its present assignment to the genus Micrococcus is also clearly inappropriate (Baird-Parker 1965). With respect to its nutrition, physiology and DNA base composition, it is likewise not assignable to the Gram-negative aerobic cocci of the genus Neisseria. A new genus is called for, and we shall make a formal proposal to this effect.

The remaining groups of Gram-negative hydrogen bacteria (B, C, D and E) consist of motile rods. The yellow pigmented strains of Group D, which include the proposed neotype strain of Niklewski's Hydrogenomonas flava (Kluyver and Manten 1942) are predominantly monotrichous, but show

a tendency to sub-polar flagellar insertion. The nonpigmented strains of Group E, which include the type strains of three species of hydrogen bacteria—H. ruhlandii, H. facilis and Pseudomonas saccharophila—show monotrichous polar flagellation. Groups D and E therefore conform reasonably well to the present definition of the genus Hydrogenomonas.

However, Groups B and C, which are the hydrogen bacteria most commonly encountered in enrichment cultures, do not fit the present definition of Hydrogenomonas. The nonpigmented strains of Group B are peritrichously flagellated rods. This very homogeneous group includes the strain originally isolated by Bovell and designated as Hydrogenomonas eutropha by Wittenberger and Repaske 1958) but of which a formal description has never been published.

The yellow pigmented strains of Group C show rather sparse flagellation, best described as "degenerately peritrichous." No named strain is included in this group; but as we shall discuss below, the organisms of Group C are the strains in our collection which most closely resemble Kaserer's description of B. pantotrophus.

Group C' comprises a collection of nonautotrophic, yellow pigmented strains, isolated from soil by aerobic enrichments at 30°C with pantothenate, trans, trans-muconate or poly-β-hydroxybutyrate as sole carbon source. In nearly all phenotypic respects except the ability to grow autotrophically with $H_2$, they are indistinguishable from the strains of Group C. Of 160 characters examined, the only other character which might serve to distinguish Groups C and C' is the ability to reduce nitrate to nitrite, possessed by all strains of Group C, and by only one of Group C'. The phenotypic resemblances between Group C and C' are so great that, in our judgement, these groups cannot be treated as separate species; at most, the recognition of two biotypes of a single species seems to be indicated. This particular example shows the undesirability of a genus defined, in whole or in part, on the basis of the ability to grow autotrophically with $H_2$. Although they are not listed in Table 1, a group of unnamed nonautotrophic pseudomonads, isolated from soil by enrichment with poly-β-hydroxybutyrate and described by Delafield et al. (1965) as their Group I shows many phenotypic similarities to H. facilis, a member of our Group E. Group A appears to have a nonautotrophic member described as Micrococcus halodenitrificans; and it would not be surprising if further work revealed the existence of nonauto-

Table 1. Some general properties of the groups studied.

| Group | No. of strains | Autotrophic growth | Cell shape | Flagellation | Carotenoid pigments | Organic C sources* | DNA Range** % G + C |
|---|---|---|---|---|---|---|---|
| A | 2 | + | cocci | none | - | 64 (55-58) | 66.3-66.8 |
| B | 14 | + | rods | peritrichous | - | 64 (53-61) | 66.3-66.8 |
| C | 11 | + | rods | degenerate peritrichous | + | 99 (51-82) | 66.8-68.4 |
| C' | 8 | - | rods | degenerate peritrichous | + | 93 (66-79) | 67.9-69.4 |
| D | 6 | + | rods | monotrichous polar or sub-polar | + | 73 (46-49) | 66.8-67.3 |
| E | 15 | + | rods | monotrichous polar | - | 88 (28-57) | 61.7-72.4 |

*Number of different organic compounds of a total of 143 tested that could be utilized as sole carbon source by any strains belonging to each group and (in parentheses) range of numbers of compounds used by individual strains.

**Determined for most strains studied, but not all strains of Group E.

Table 2. Some distinguishing physiological characters of major groups studied.

| | A | B | C | C' | D | E |
|---|---|---|---|---|---|---|
| Denitrification | + | +* | - | - | - | - |
| Extracellular hydrolysis of poly-β-hydroxybutyrate | - | - | + | + | - | v |
| Growth with: | | | | | | |
| sarcosine, creatine | + | - | - | - | - | - |
| testosterone | - | + | - | - | - | - |
| pantothenate** | - | - | + | + | - | - |
| *meta*-hydroxybenzoate | + | + | + | + | (+) | - |
| hydroxymethylglutarate | - | + | + | + | - | v |
| Pathway of *meta*-hydroxybenzoate metabolism | *pr* | *ge* | *pr* | *pr* | *pr* | - |
| Cleavage of protocatechuate*** | *o* | *o* | *o* | *o* | *m* | v |
| Ketolactose production | - | - | (+) | (+) | - | - |
| Cytochrome $a_2$ (p 625 mμ)**** | - | - | + | + | - | - |

KEY: + Positive
- Negative
(+) Positive for most strains
v Variable
*pr* *Via* protocatechuate
*ge* *Via* gentisate
*o* *Ortho*
*m* *Meta*

*May be slow or lost after prolonged aerobic cultivation on organic media.

**May require mutation for expression.

***Protocatechuate cleavage was tested in the intermediary metabolism of *p*-hydroxybenzoate, *m*-hydroxybenzoate and quinate for each strain capable of using any one of these compounds for growth, except that only *p*-hydroxybenzoate and quinate were used for Group B.

****Tested in representative strains only.

trophic counterparts of the hydrogen bacteria belonging to Groups B and D as well. All these facts lend additional support to the conclusion that a genus with the definition of Hydrogenomonas is undesirable on both determinative and scientific grounds.

We wish now to discuss another question which bears on the taxonomic legitimacy of the name Hydrogenomonas: the possibility of maintaining its type species on the basis of a neotype strain. Since B. pantotrophus was described as having yellow cellular pigments, only our Groups C and D might possibly represent it. Of the two, Group C is clearly the better candidate for recognition as B. pantotrophus. Particularly suggestive are the slimy growth, the unusually long flagella, and the production of a characteristic, unpleasant odor by autotrophically grown cultures. Kaserer described this odor as that of "soapy water in a laundry"; and two persons familiar with traditional European laundering practice confirmed the aptness of this description for the odor of our cultures of Group C. In three respects, however, the strains of Group C do not conform to Kaserer's description. One dissimilarity, the degenerately peritrichous flagellation of our strains, is not in itself conclusive. As Kaserer pointed out, the flagella of B. pantotrophus are hard to stain, and it is difficult to determine their exact mode of insertion because of the capsules that surround the cells. Our own initial impression from examining flagella stains of the strains of Group C was that flagellar insertion was polar, and monotrichous; and it was only after doubts on this point had been expressed by Dr. M. P. Starr, who also examined these strains, that a more systematic and careful examination led us to conclude that the flagellation was in reality degenerately peritrichous. Dr. E. Leifson also examined our strains and classified them as peritrichous. None of the strains of Group C agree with Kaserer's description of B. pantotrophus with respect to the utilization of sucrose and the reduction of nitrate. Special attempts to isolate sucrose-utilizing strains of Group C by successive enrichment with hydrogen and with sucrose consistently failed. Some strains of Group D can utilize sucrose, but do not have the special odor, the long flagella or the slimy growth habit which Kaserer described for B. pantotrophus. One polarly flagellated, yellow pigmented strain, received from the U. S. S. R., which had been tentatively identified by Zavarsin as H. pantotropha, did not use sucrose, possess long flagella or produce a characteristic odor; it is

a member of a well-defined subgroup in Group D. From the foregoing discussion, it is clear that none of the yellow pigmented strains of hydrogen bacteria in our collection (17 well characterized strains and a number of partially characterized ones) can be identified with any confidence as H. pantotropha. If a strain of Group C were to be designated as the neotype, it would be necessary to revise Kaserer's description of B. pantotrophus with respect both to structural and to physiological characters. Furthermore, the inclusion of the strains of Group C' as a biotype of this species would eliminate hydrogen utilization as a specific character of H. pantotropha. It has been previously suggested (Nabokich and Lebedeff 1907; Niklewski 1910; Kluyver and Manten 1942) that the original description of B. pantotrophus may have been based on the study of a mixed culture, and our data certainly do not contradict this possibility. For all these reasons, we consider it desirable to treat Hydrogenomonas pantotropha (Kaserer) Orla-Jensen as a nomen dubium; and we shall assign the strains of our Groups C and C' to a single species. Since the genus Hydrogenomonas as originally described was monotypic, the lack of a recognizable type species makes the generic name a nomen nudum. On these grounds, we eliminate it from consideration as a possible generic name for any of the rod-shaped hydrogen bacteria. We are therefore faced with the problem of finding appropriate generic locations for the organisms belonging to Groups B, C, C', D and E.

All hydrogen bacteria of Groups D and E, which include the named species H. flava, H. ruhlandii, H. facilis and P. saccharophila, as well as a number of unnamed but clearly distinct strains, are readily assignable by virtue of their polar flagellation, DNA base composition and general phenotypic properties to the genus Pseudomonas (Stanier et al. 1966). The strains of Groups B, D and C' are, however, excluded from this genus as now defined by their modes of flagellar insertion. On the basis of this structural character, they must be assigned to one (or two) genera of aerobic, chemoorganotrophic, Gram-negative rods bearing peritrichous or degenerately peritrichous flagella and characterized by DNA of a relatively high G + C content. The correct generic assignment of bacteria having this constellation of properties is at present very difficult, largely bacause of the lack of a single, broadly defined genus with a well established type species, which can accommodate the peritrichously flagellated counterparts of Pseudomonas. Instead,

Table 3. Flagellar arrangement in representative strains.

| Group | Strain | Number of flagella per cell | | | | Origin of each flagellum | | |
|---|---|---|---|---|---|---|---|---|
| | | Average | Percent of all cells counted possessing | | | Percent of all flagella counted | | |
| | | | 1 | 2 | 3 or more | Polar | Sub-polar | Lateral |
| B | ATCC 17697 | 2.70 | 20 | 29 | 51 | 30 | 45 | 25 |
| C | ATCC 17713 | 1.54 | 62 | 25 | 13 | 32 | 48 | 20 |
| C' | ATCC 17549 | 1.55 | 65 | 20 | 15 | 30 | 51 | 19 |
| D | *H. flava* | 1.06 | 94 | 6 | 0 | 69 | 24 | 7 |
| | ATCC 17724 | 1.02 | 98 | 2 | 0 | 83 | 14 | 3 |
| E | ATCC 17695 | 1.02 | 98 | 2 | 0 | 98 | 1 | 1 |

The cultures were grown in complex medium at 30 C. Between 100 and 150 flagellated cells of each strain, the origin and number of whose flagella could be interpreted, were included in each count.

a choice must be made among several genera which are poorly defined and in some cases lack recognizable type species. These genera include: Alcaligenes, Achromobacter, Flavobacterium, Agrobacterium and Rhizobium. Agrobacterium and Rhizobium, each of which has a good type species, are primarily defined and distinguished by the special mutualistic or parasitic relations of their members to plants. Neither of these genera appears, accordingly, to be an appropriate location for hydrogen bacteria of groups B, C and C'. On the grounds of pigmentation, groups C and C' should be assigned to Flavobacterium. However, this genus does not have a recognizable type species and at least some of the organisms now placed in it are gliding bacteria of low G + C content, more correctly assignable to Cytophaga (O. B. Weeks, personal communication). In view of the dubious current status of Flavobacterium, it appears imprudent to assign any newly described species to this genus. On the grounds of lack of cellular pigmentation, Group B could be assigned to Achromobacter. However, according to Drs. J. M. Shewan and A. J. Holding (personal communication), "Achromobacter is almost irretrievable due to the absence of a culture that even approximates the characteristics of A. liquefaciens" (viz., its type species). Drs. Shewan and Holding have informed us that the type species of Alcaligenes, A. fecalis, is a well defined and readily recognizable organism. By elimination, accordingly, the only existent genus to which the bacteria of groups B, C and C' can safely be assigned is Alcaligenes.

Formal taxonomic proposals:

Paracoccus Davis, gen. nov.

Gram-negative, nonsporeforming, immotile cocci. Strictly aerobic, except in media with nitrate, in which anaerobic growth may be supported by denitrification. Metabolism respiratory, not fermentative. Oxidase and catalase positive. Arginine dihydrolase negative. Heterotrophic, or facultatively autotrophic with the aerobic oxidation of $H_2$ as source of energy. The guanine + cytosine content of the DNA is in the neighborhood of 65-67 moles percent.

Type species: Paracoccus denitrificans (Beijerinck and Minkman 1910) Davis comb. nov. Syn: Micrococcus denitrificans Beijerinck and Minkman (1910). Holotype strain: ATCC 17741; received from C. B. van Niel as the type strain of Micrococcus denitrificans Beijerinck. This may represent the same original isolate as ATCC 19367 and ATCC 13543 from the Delft collection.

Table 4. Proposed taxonomic allocation of hydrogen bacteria and related strains.

| Group | Proposed generic allocations | Species included | Type strain | DNA: % G + C |
|---|---|---|---|---|
| A | *Paracoccus* Davis *gen. nov.* | *P. denitrificans* (Beijerinck & Minkman, 1910) Davis. *gen. nov.; comb. nov.* | ATCC 17741 | 66.3 |
| B | *Alcaligenes* Castellani and Chalmers | *A. eutrophus* (Wittenberger & Repaske, 1958) Davis. *sp. nov.* | ATCC 17697 | 66.8 |
| C and C' | *Alcaligenes* | *A. paradoxus* Davis. *sp. nov.* | ATCC 17713 | 68.4 |
| D | *Pseudomonas* Migula | a) *P. flava* (Niklewski, 1910) Davis. *comb. nov.* | Lab. voor Microbiologie, Delft The Netherlands | 67.3 |
| | | b) At least one unnamed species | | |
| E | *Pseudomonas* | a) *P. saccharophila* Doudoroff, 1940 | ATCC 15946 | 68.9 |
| | | b) *P. ruhlandii* (Packer & Vishniac, 1955) Davis. *comb. nov.* | ATCC 15749 | not determined |
| | | c) *P. facilis* (Schatz & Bovell, 1952) Davis. *comb. nov.* | ATCC 17695 | 63.8 |
| | | d) Several unnamed species | | |

The type species is described in Bergey's Manual (7th edition). Additional specific characters include: DNA composition, 66.3-66.8% G + C; poly-β-hydroxybutyrate as intracellular carbon reserve; ability to grow with sucrose, trehalose, maltose, glycerate, m-hydroxybenzoate, p-hydroxybenzoate and histidine as sole carbon sources; dissimilation of aromatic compounds through ortho cleavage of intermediate diphenols.

The nonautotrophic, halophilic species M. halodenitrificans Robinson and Gibbons (1952), conforms to the above generic description, and it is tentatively proposed to include it as a separate species of the genus.

Alcaligenes eutrophus (Wittenberger and Repaske 1958) Davis sp. nov.

Gram-negative rods, 1.8-2.6 x 0.7 μ during exponential growth; 1.0 x 0.7 μ in stationary phase. Nonsporeforming. Motile by one to four (rarely 5 or more) peritrichous flagella. DNA base composition: G + C, 66.3-66.8 moles percent. Obligately aerobic, except in mineral media with nitrate, where denitrification may occur. (Denitrification is observed in mineral medium with lactate but not in complex media or under autotrophic conditions; may be lost after prolonged cultivation on organic media). Do not ferment carbohydrates or possess arginine dihydrolase. Nitrite is accumulated. Oxidase positive, catalase positive. Heterotrophic, but facultatively autotrophic in atmospheres containing hydrogen, oxygen and $CO_2$. Use a wide variety of organic compounds as sole carbon sources, including testosterone, phenol, benzoate, meta- and para-hydroxybenzoate, caproate, glycollate, norleucine, nicotinate and trigonelline. Do not utilize ethanol, glycerol, mannitol, pentoses, disaccharides, D-tryptophan, or acetamide. Fructose is the only sugar used by strains upon initial isolation from nature (by enrichment for "hydrogen bacteria") but glucose-utilizing mutants can be obtained from all strains. meta-Hydroxybenzoate is metabolized via the gentisate pathway; para-hydroxybenzoate via the ortho cleavage of protocatechuate. Accumulate poly-β-hydroxybuturate as intracellular carbon reserve. Do not hydrolyze gelatin or starch. Colonies are opaque and white or cream-colored, becoming brownish after several days. Among the commonest soil and water bacteria isolated by enrichment with hydrogen; optimum temperature, about 30°C.

Holotype strain: ATCC 17697 isolated by Bovell (1957) and subsequently called H. eutropha by Wittenberger and

Repaske (1958; 1961), but never legitimately described. (Received from Dr. Repaske, National Institutes of Health, Bethesda, Maryland). This strain is the same as Hydrogenomonas H20 of Dr. H. G. Schlegel. Other representative strains include ATCC 17698 and 17699 designated as Hydrogenomonas H1 and H16, respectively, by Dr. H. G. Schlegel. Synonym: Hydrogenomonas eutropha Wittenberger and Repaske (1958) illegit.

Alcaligenes paradoxus Davis sp. nov.

Gram-negative, nonsporeforming rods, 1.5-2.6 x 0.5 μ during exponential growth, multiplying by binary transverse fission, and occurring singly or in pairs. Generally capsulated and motile; "degenerately peritrichous," possessing one or two (rarely 3 or 4) flagella with predominantly subpolar or lateral insertion. The flagella are fragile and characteristically four to six times as long as the cell. Pigmented, possessing "neutral" or saponifiable carotenoid pigments with absorption maxima at ca. 405 and/or 425 mμ in acetone. Obligately aerobic; incapable of denitrification, of fermenting sugars or decomposing arginine. Oxidase positive, possessing cytochromes of the a, b and c types, including a cytochrome $a_2$ with a peak at 625 mμ in the reduced/oxidized spectrum. Catalase positive. Heterotrophic or facultatively autotrophic.

All strains can use a wide variety of organic compounds as sole carbon sources. Many strains (biotype I) can use the aerobic oxidation of molecular hydrogen as a source of energy for autotrophic growth. Other strains (biotype II) do not grow autotrophically or oxidize hydrogen. Can use nitrate but not atmospheric $N_2$ as nitrogen source. Not known to be plant parasites or symbionts. DNA composition in the range of ca. 68-70 moles percent G + C. Accumulate poly-β-hydroxybutyrate as intracellular carbon reserve.

Extracellular poly-β- hydroxybutyrate and sorbitan monooleate (Tween 80) are hydrolyzed by all strains, gelatin by rare strains, and starch by none.

Among the hundred or more organic compounds used by some strains belonging to the species, characteristic carbon sources used by all or most strains include: pantothenate (growth with which may require the selection of mutants), glycollate, malonate, sebacate, mesaconate, hydroxymethylglutarate and sorbitol. All strains use glucose, fructose, mannose, galactose, and L-arabinose, and most strains use various D-pentoses and D-fucose. Sucrose and trehalose are

not utilized. Acid is produced aerobically in complex media with glucose. Most strains oxidize lactose to 3-ketolactose (Bernaerts and DeLey 1958) and a few can use lactose as carbon source. Both meta- and para-hydroxybenzoate are metabolized via the ortho cleavage of protocatechuate.

Colonies tend to be glistening and slimy, yellow or greenish yellow in color.

The species is a common soil inhabitant. Optimal temperature, about 30°C.

Holotype ATCC 17713 (Biotype I), isolated from Berkeley, California soil in mineral medium with an atmosphere of 91% $H_2$, 4% $O_2$ and 5% $CO_2$.

Biotype I. Facultatively autotrophic; reduce nitrate to nitrite in organic media. Commonest pigmented organisms isolated by enrichment for "hydrogen bacteria." Strains enriched and isolated with low partial pressures of $O_2$ may initially show the phenomenon of "oxygen sensitivity" in that they do not grow autotrophically with 20% $O_2$. Such strains, however, produce mutants that are indistinguishable with respect to oxygen sensitivity from those initially isolated with 20% or 30% $O_2$. Autotrophically grown cultures produce a characteristic unpleasant odor. This biotype is represented by the holotype strain of the species, as well as by strains ATCC 17712, 17715, 17716, 17722, and 17723.

Biotype II. Nonautotrophic; rarely reduce nitrate to nitrite in organic media. Isolated from soil by enrichment with pantothenate, trans, trans-muconate or poly-β-hydroxybenzoate as sole carbon sources.

Typical strain: ATCC 17549 (Strain $P_2$-106-S(3)) isolated by Goodhue and Snell (1966) and studied by them for its metabolism of pantothenate.

Other strains: ATCC 17716, 17719, 11720.

A complete description of the nutritional and physiological properties of the individual strains of the species described above and of the polarly flagellated ones will be published elsewhere.

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