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Classification of *Desulfovibrio* Species, the Nonsporulating Sulfate-reducing Bacteria

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INTRODUCTION

In an earlier publication (7), we reclassified the sporeforming, dissimilatory sulfate-reducing bacteria, and proposed a new genus, *Desulfotomaculum*, with three species: *D. nigrificans*, *D. orientis*, and *D. ruminis*. Sufficient data have now been published to warrant a comparable reassessment of the classification of the nonsporulating, dissimilatory sulfate-reducing bacteria which remain in the genus *Desulfovibrio*.

TAXONOMIC CRITERIA

We have taken bacteria capable of anaerobic growth in a medium based on sodium lactate and sulfate, with concomitant dissimilatory reduction of the sulfate to sulfide, as true dissimilatory sulfate-reducing bacteria, assignable to one of the two genera, *Desulfovibrio* or *Desulfotomaculum*.

For classification within the genus *Desulfovibrio*, we have taken the following properties as taxonomically significant. *Absence of sporulation:* based on data supplied by the original investigator, when available. *Deoxyribonucleic acid (DNA) composition:* based primarily on the data of Saunders, Campbell, and Postgate (28) supplemented by those of Sigal et al. (32). *Desulfoviridin:* indicated by a positive fluorescence test (22). One strain (Norway 4) is known that does not contain desulfoviridin but has all the other characters of *Desulfovibrio* (19). *Polar flagellation:* either single or lophotrichous, based on our own data as well as those supplied by the original investigator; usually associated with progressive motility. *Cytochrome c_3:* indicated by an absorption band at 552 to 554 mμ, forming a "pyridine hemochromogen" of the hematoheme class, observed either by ourselves or other investigators.

Assignment to the species proposed herein has been made on the basis of the following properties. *Growth with certain carbon sources:* the substrates pyruvate, malate, choline, oxamate, acetate, propionate, and butyrate were taken as taxonomically significant. Growth tests with sulfate were made either in medium C of Butlin et al. (4) or in Starkey's medium (33) supplemented with yeast extract (0.1%) and Na_2S (1 to 2 mM). For marine strains the media also contained 2.5% NaCl. Growth was accepted as positive only if it remained in excess of the yeast extract blank for two or more subcultures. Growth tests without sulfate were performed with Postgate's sulfate-deficient medium (21); Na_2S was not added, thus avoiding contamination by the Na_2SO_4 normally present in commercial Na_2S. Growth for at least four subcultures was accepted as evidence of sulfate-free growth. With choline, a smell of trimethylamine provided a confirmatory indication of growth. *Hibitane resistance* was based mainly on the data of Saleh (27), supplemented by unpublished data provided by J. D. A. Miller. These data often show a good correspondence with the DNA composition,

TABLE 1. *Simplified key to the classification of the dissimilatory sulfate-reducing bacteria, following the scheme of Campbell and Postgate (7) and that proposed here*

Character	Desulfotomaculum			Desulfovibrio				
	nigrificans	*orientis*	*ruminis*	*desulfuricans*	*vulgaris*	*salexigens*	*africanus*	*gigas*
Form	Rod	Curved rod	Rod	Vibrio	Vibrio	Vibrio	Sigmoid vibrio	Spirillum
Flagella	Peritrichous	Peritrichous	Peritrichous	Single, polar	Single, polar	Single, polar	Lophotrichous	Lophotrichous
Spores	+	+	+	−	−	−	−	−
Type of cytochrome	*b*	*b*	*b*	c_3	c_3	c_3	c_3	c_3
Desulfoviridin	−	−	−	+	+	+	+	+
% G + C in DNA	44.7	41.7	45.6	55.3 ± 1	61.2 ± 1	46.1 ± 1	61.2 ± 1	60.2
Growth in;								
Pyruvate minus sulfate	+	−	+	+	−	−	−	−
Choline minus sulfate				+	−	−	−	−
Malate plus sulfate				+	−	+	+	−
Formate plus sulfate	−	−	+					
Acetate plus sulfate	−	−	−	−	−	−	−	−
NaCl requirement	−	−	−	−	−	+	−	−
Hibitane resistance (mg/liter)	0.25	0.25	1	10–25	2.5	1,000	2.5	2.5
Thermophily	+	−	−	−	−	−	−	−

though a small number of exceptions has been observed since the publication of Saleh's paper. *Salt requirement:* failure to grow in Baars' medium (1) supplemented with yeast extract and Na_2S, but without 2.5% NaCl, was accepted as evidence for an obligate salt requirement. Ability to grow with approximately iso-osmolar KCl but not Na_2SO_4 (16) was taken as evidence for a specific chloride ion requirement. *Morphology* was examined by phase-contrast light microscopy and by electron microscopy.

The following tests were not given taxonomic value. *Utilization of carbon sources,* other than those listed above, because of divergencies in both published and unpublished data in different laboratories. *Motility:* of the two nonmotile strains known to investigators in this field, Teddington R (NCIB 8302) and Holland D6 (NCIB 8311), the former has recently been shown to be motile in special circumstances (R. Lanigan and J. D. A. Miller, *personal communications*) and the latter has not been studied exhaustively. *Fumarate utilization:* ability to perform "sulfate-free" growth with fumarate, analogous to that with pyruvate or choline, has been observed in certain strains by J. D. A. Miller. The occurrence of this property in the strains so far studied shows no clear correlation with the classification proposed here. *Serology:* sufficient serological data are not yet available for use with *Desulfovibrio* in the manner that was used with the sporeforming types (5, 26). Such unpublished data as we have are wholly consistent with the scheme proposed here.

Our scheme is presented formally and followed by a commentary; Table 1 gives a simplified key to our general classification of sulfate-reducing bacteria.

DESCRIPTION OF THE GENUS DESULFOVIBRIO

Genus **Desulfovibrio** (Kluyver and van Niel, 13) Postgate and Campbell. L. pref. *de* from; L. noun *sulfur* sulfur; L. v. *vibro* to vibrate; M. L. mas. n. *Vibrio* that which vibrates, a generic name; M. L. mas. n. *Desulfovibrio* a vibrio that reduces sulfur compounds. [The name, being Latin, is spelled with "f." *Desulphovibrio desulphuricans* is incorrect.]

Nonsporulating, gram-negative vibrios, sometimes sigmoid or spirilloid; occasionally straight.

[Morphological descriptions refer generally to a freshly grown culture in Baars' medium (1), if necessary containing 0.02 to 0.1% yeast extract, and if necessary containing 2.5% NaCl. The cultural conditions must be specified since bacterial morphology is influenced by the environment.] Obligate anaerobes with polar flagella showing progressive motility. Mesophilic, sometimes halophilic. Contain cytochrome c_3 and desulfoviridin. Hydrogenase usually present. Facultative or obligate sulfate-reducers; sulfate reduction is their respiratory dissimilatory process. Autotrophic growth on hydrogen has not been critically demonstrated (17, 23, 25). Members generally show some degree of antigenic cross-reaction. Pathogenicity not recorded. Found in seawater, marine mud, freshwater, and soil. The type species is *Desulfovibrio desulfuricans* (Beijerinck; Kluyver and van Niel) Postgate and Campbell.

Species of Which Cultures Exist in Recognized Collections

1. **Desulfovibrio desulfuricans** (Beijerinck, 3; Kluyver and van Neil, 13) Postgate and Campbell. Generic synonyms include *Spirillum* (Beijerinck 3), *Microspira* (Migula, 18), *Vibrio* (Baars, 1), and *Sporovibrio* (Starkey, 33). Synonym: *Vibrio cholinicus* (Baker, Papiska, and Campbell, 2; Senez and Pascal, 31).

desulfuricans. L. pref. *de* from; L. noun *sulfur* sulfur; M. L. *desulfuricans* reducing sulfur compounds.

Morphology: Vibrios, 3 to 5 by 0.5 to 1 μ; rapid progressive motility by a single polar flagellum; sigmoid forms may occur.

Culture: Obligately anaerobic, requiring an E_h less than -100 mv for growth at *p*H 7.2. Temperature range: 28 to 44 C. Usually requires special media containing sulfates. Does not form gas from carbohydrates. Produces round, wholly black colonies in lactate-sulfate-agar containing excess of a ferrous salt; colonies in peptone-glucose-sulfate-agar similar, but show a golden sheen in the earliest stages of development.

Carbon sources: Utilizes lactate, malate, pyruvate, and choline but not oxamate, oxalate, acetate, propionate, or butyrate; acetate accumulates as the end product of oxidation of most carbon sources and sulfate is reduced.

Malate: Usually supports growth if sulfate is present.

Choline: Usually supports growth either in the presence or in the absence of sulfate.

Pyruvate: Usually supports growth either in the presence or in the absence of sulfate.

Gelatin: Not liquefied.

Nitrates: Not reduced.

Pigments: Cell suspensions show characteristic absorption bands of cytochrome c_3 at 525 and 553 mμ, and of desulfoviridin at 630 mμ.

Fluorescence: Concentrates of the bacteria fluoresce red in light of 365 mμ if inspected immediately after addition of a few drops of 2.0 N NaOH. This reaction releases the chromophore of desulfoviridin.

Hibitane resistance: 10 to 25 mg/liter. [Minimal inhibitory concentration; growth occurred with one-half of this concentration (27).]

DNA base composition: 55.3 $\pm$ 1% guanine plus cytosine (G + C).

Source: Freshwater, particularly polluted waters showing blackening and sulfide formation; soils, particularly anaerobic or waterlogged soils rich in organic material; marine and brackish waters.

Holotype: Lost. Proposed *neotype*: Strain Essex 6 (NCIB 8307). Other strains of this species include "*Vibrio cholinicus*" (ATCC 13541).

Varieties

D. desulfuricans var. *aestuarii*. Strains of marine or brackish origin capable of becoming adapted to freshwater environments have sometimes been assigned to this subspecific variety but are not accepted. Strain Sylt 3 (NCIB 9335) does not adapt to freshwater media and is probably a legitimate variety since the character seems stable.

D. desulfuricans var. *azotovorans*. Capable of fixing gaseous nitrogen. Often rod-shaped; does not grow with choline minus sulfate. Type strain: Berre eau (NCIB 8387); second strain: Berre sol (NCIB 8388).

2. **Desulfovibrio vulgaris** Postgate and Campbell.

vulgaris. L. adj. *vulgaris* common.

Description similar to that of *D. desulfuricans* except:

Carbon sources: Carbon sources restricted to lactate, pyruvate, formate, and certain simple primary alcohols.

Malate: Does not support growth.

Choline: Not metabolized.

Pyruvate: Does not support growth without sulfate.

Hibitane resistance: 2.5 mg/liter.

DNA base composition: 61 $\pm$ 1% G + C.

Source: As for *D. desulfuricans*.

Holotype: Strain Hildenborough (NCIB 8303); another strain is Wandle (NCIB 8305).

Varieties

D. vulgaris var. *oxamicus*. Capable of metabolizing oxamate or oxalate. This variety is aberrant in showing sulfate-free growth with choline or

pyruvate. Type strain: Monticello 2 (NCIB 9442; Postgate, 24).

3. **Desulfovibrio salexigens** Postgate and Campbell. Syn. *Microspira aestuarii* (van Delden, 35).

salexigens. L. noun *sal* salt; M.L. *exigens* to demand; M.L. *salexigens* salt-demanding. The obligate saltwater species.

Morphology: As for *D. desulfuricans.*

Culture: As for *D. desulfuricans* except that NaCl in excess of 0.6% (usually 2.5 to 5%) is essential for growth. The required component of NaCl is the chloride ion.

Carbon sources: As for *D. vulgaris* except for malate utilization.

Malate: Supports growth if sulfate is present.

Choline: No growth with or without sulfate.

Pyruvate: No growth in the absence of sulfate.

Hibitane resistance: Variable, often more than 1 g/liter.

DNA base composition: 45.5 ± 1.0% G + C.

Other data as for *D. desulfuricans.*

Source: Seawater, marine or estuarine muds, pickling brines.

Holotype: Strain British Guiana (NCIB 8403); another strain is California 43:63 (NCIB 8364).

4. **Desulfovibrio gigas** (LeGall, 14) Postgate and Campbell.

gigas. L. noun *gigas* giant. A "giant" sulfate-reducing spirillum isolated from a marine tidal lake (14).

Morphology: Large curved rods, 5 to 10 by 1.2 to 1.5 μ, often in chains as spirilla. Polar lophotrichous flagella, progressive slow motility. Young organisms show areas of low contrast when examined by phase microscopy.

Culture: As for *D. desulfuricans* but an E_h of about 80 mv (ascorbate at *p*H 7) seems most suitable for growth. Growth is slower than that of other species.

Carbon sources: As for *D. vulgaris* except that metabolism of alcohols is not recorded.

Choline: No growth with or without sulfate.

Pyruvate: Growth only with sulfate.

DNA base composition: 61% G + C.

Other data as for *D. desulfuricans.*

Source: Etang de Berre, near Marseille, France. Despite its saltwater origin, saline media are not used for its culture.

Holotype: D. gigas (NCIB 9335).

5. **Desulfovibrio africanus** Campbell, Kasprzycki, and Postgate (6).

africanus. L. adj. *africanus* pertaining to Africa. Slender, lophotrichous vibrios originally obtained from two sites in Africa (seawater from Walvis Bay and freshwater from a spring at Benghazi).

Morphology: Long, sigmoid rods, 5 to 10 by 0.5 μ. Polar lophotrichous flagella, rapid progressive motility.

Culture: As for *D. vulgaris.* Has wide salt tolerance.

Carbon sources: As for *D. vulgaris* but grows with malate if sulfate is present.

Hibitane resistance: As for *D. vulgaris.*

DNA base composition: 60 ± 1% G + C.

Source: Saltwater or freshwater from Africa.

Holotype: Strain Benghazi (NCIB 8401). A saltwater strain, capable of growth in freshwater, is Walvis Bay (NCIB 8397).

NONSPORULATING SPECIES OF UNCERTAIN STATUS

Desulfovibrio rubentschikii. Habitat, morphology, and culture described by Baars (1) as similar to *D. desulfuricans.* Distinguished by its ability to oxidize its carbon sources beyond the fatty acid level to CO_2 and water, and to grow with acetate, propionate, or butyrate as sole carbon source. *D. rubentschikii* var. *anomalous* was similar but unable to utilize acetate; propionate and butyrate were utilized.

Desulphoristella hydrocarbonoblastica (Hvid, 8).

Source: A subterranean water in Sjaelland, Denmark.

Morphology: Short, pointed, nonmotile, nonsporulating rods 1 to 2 by 0.7 to 1 μ (in a formate-sulfate medium).

Culture: Obligate anaerobe, facultative autotroph; grew best at 30 C, did not grow at 37 C.

Nutrition: Utilized formate, lactate, propionate, or acetate; also other organic compounds.

Hydrocarbon formation: Old cultures sometimes contained an ether-soluble bituminous material.

COMMENTARY

We recognize that our scheme for the genus *Desulfovibrio* is less clear-cut than our earlier proposal for *Desulfotomaculum*, and that, particularly in certain categories of drug resistance and carbon utilization, new data may be forthcoming that will necessitate further taxonomic revision. We present these proposals as a working classification of the strains so far known to us. Table 2 lists most of the strains at present available from recognized culture collections, with their classification according to our scheme. A detailed discussion of our nomenclature follows.

D. desulfuricans. Beijerinck (3) used lactate or malate as the carbon source for his media. Growth on malate would have excluded the type of organism listed as *D. vulgaris*; hence, Beijerinck's description gives taxonomic priority to the facultative sulfate-reducing bacteria: those generally

TABLE 2. *Assignment of strains of Desulfovibrio to the specific groups proposed*[a]

Desulfovibrio desulfuricans
Essex 6 (8307), America (8372; ATCC 7757), "Vibrio cholinicus" (9467), Canet 20 (8391), Canet 40 (8363), Canet 41 (8393), El Agheila Z (8380), Venice 1 (8322), Norway 4 (8301),[b] Teddington R (8312),[c] California 29:137.5 (8326), El Agheila 4 (8396), Aberdovey (9492), California 29:137.11 (8339), Hossegor (8400), Byron (8458)
var. *aestuarii*: Sylt 3 (9335)
var. *azotovorans*: Berre eau (8387), Berre sol (8388)

Desulfovibrio vulgaris
Hildenborough (8303), Wandle (8305), Beckton (8319), Marseille gaz 54 (8386), Teddington M (8302), Llanelly (8446), Holland D6 (8311),[c] El Agheila A (8309), Woolwich (8457), Venezuela (8399), Denmark (8456). Also a strain provided by Professor Furusaka.
var. *oxamicus*: Monticello 2 (9442)

Desulfovibrio salexigens
British Guiana (8403), Avonmouth (8398), Louisiana 43:11 (8365), California 43:63 (8364), El Agheila C (8308), El Agheila 2 (8402),[d] New Jersey SW8 (8315),[d] New Jersey SW3 (8316),[d] Australia (8329),[d] strain Maizuru of Kadota (reference 11).

Desulfovibrio gigas
Le Gall's original strain (9332)

Desulfovibrio africanus
Benghazi (8401), Walvis Bay (8397)

[a] The holotype or neotype strain is placed first. Strain names are followed by their number in the National Collection of Industrial Bacteria, Aberdeen, Scotland, unless otherwise indicated. Aberrations from the key given in Table 1 are indicated in footnotes.

[b] Desulfoviridin absent.

[c] Rarely motile.

[d] Hibitane resistance atypically low.

capable of growth without sulfate if pyruvate or choline is the carbon source. Thus, the "Hildenborough" strain, which has been the subject of much physiological research, is excluded from the type species. The neotype species suggested is a freshwater strain. Ability to show sulfate-free growth with pyruvate or choline is a characteristic of most members of this group, though some exceptions have been observed.

D. desulfuricans var. *aestuarii*. "*Desulfovibrio aestuarii*" differed from *D. desulfuricans*, according to van Delden (35), in its marine origin. Since both *D. aestuarii* and *D. desulfuricans* grew readily with 1.5% NaCl, he expressed reservations about regarding the marine type as a separate species. Baars (1) and Kluyver and Baars (12) considered that the marine and freshwater types were readily interconverted by "training," but Rittenberg (Ph.D. Thesis, Univ. California, 1941) was unable to train his marine strains to grow in freshwater media (though, like van Delden's strains, they grew readily with 1.5% NaCl). Strains with salt optima much above 3% have been reported (11, 37), including the strain of Iya and Sreenivasaya (10) that had a range of 0 to 13% NaCl with an optimum at 6%, and the marine Canet 41 strain of Senez which grew with 0 to 12% NaCl (30). Littlewood and Postgate (16) and Ochynski and Postgate (20) reexamined this question. Their marine and freshwater strains differed mainly in the distribution of organisms in a culture able to grow with various salt concentrations. In general, marine strains showed three classes of behavior: one type grew readily without NaCl; another type required training in the sense that only a few of the population grew immediately without salt. These types thus showed no stable difference from the freshwater types of *D. desulfuricans*. Stüven's strain Sylt 3, however, has all the properties of the *D. desulfuricans* group plus a stable salt requirement (34; and confirmed in our own tests). We have therefore assigned this strain variety status within that group. Littlewood and Postgate's third type (16) did not grow without NaCl and could not be trained to do so; it forms the species now named *D. salexigens* and is discussed further below.

The freshwater strains of *D. desulfuricans* chosen by Littlewood and Postgate (16), and later by Ochynski and Postgate (20), for study are, with one exception, strains that would here be classified as *D. vulgaris*. Hence, a detailed examination of a freshwater *D. desulfuricans* has not been made. Ochynski and Postgate (20) trained strain Essex 6 (NCIB 8307), a freshwater *D. desulfuricans*, to grow in media of 2.5% NaCl.

D. desulfuricans var. *azotovorans*. The majority of laboratory stock cultures of *Desulfovibrio* spp. do not fix atmospheric N_2. The two nitrogen-fixing strains at present available from recognized culture collections, isolated by LeGall, Senez, and Pichinoty (15), are morphologically unusual in being straight rods. These two characters are probably sufficient to justify "variety" status.

D. vulgaris. Into this group have been placed the obligate sulfate-reducing bacteria: those distinguished by their inability in any known circumstance to grow without sulfate and by the high G + C content of their DNA.

D. vulgaris var. *oxamicus*. Postgate's oxamate-utilizing strain (24) Monticello 2 (NCIB 9442) presents a taxonomic problem. Its DNA composition, hibitane resistance, and morphology place it with the *D. vulgaris* group. It grows, however,

without sulfate if choline or pyruvate is provided, and in this character resembles *D. desulfuricans*. Its ability to metabolize oxamate or oxalate appears to be unique. We have given greater weight to the characters it shares with the *D. vulgaris* group and have classified it as a variety.

D. salexigens. This group consists, so far, of obligate salt-requiring types, being distinguished from *D. desulfuricans* var. *aestuarii* in requiring the chloride ion, not the sodium ion, for growth. A low G + C content in the DNA, an inability to adapt to freshwater, absence of choline metabolism, and high hibitane resistance typifies this group; a blue oxido-reducible pigment found in old cultures distinguishes the type strain from the rest of the group. Members of this group are particularly prone to form the coccoid bodies described by Butlin et al. (J. Gen. Microbiol. **3**:iii, 1949). Sufficient of these characters seem permanent enough to justify specific separation. The name "salexigens" may not be a wise choice, since a freshwater organism having the other characters of this group may yet be discovered; however, the fact that all known strains in this group are of saltwater habit may justify taking this taxonomic risk.

D. gigas. This species is represented by a single isolate (14). Morphologically, it is spectacularly different from all other desulfovibrios; it has a close resemblance to a spirillum, even to its flagellation, yet it retains the physiological characteristics and pigments of this genus and the DNA composition of the *D. vulgaris* group.

D. africanus. The morphology of this group is consistently different from that of those discussed earlier, both in size of the cell and in number of polar flagella. They are most closely akin to the *D. vulgaris* group, and may represent an intermediate between this and *D. gigas*. The taxonomic weight which should be placed on their ability to use malate is uncertain. The readiness with which strain Walvis Bay (of marine origin) grows in freshwater media indicates that salt relations are not of taxonomic significance in this group.

NOMINA REJICENDA

Desulfovibrio rubentschikii. The main distinguishing feature of this species would be its ability to utilize acetate for sulfate reduction and thus to metabolize its carbon nutrients more efficiently. Baars (1) believed that the species was fairly widespread, but despite repeated attempts by various workers such an organism has not so far been obtained (29), and inquiries elsewhere have always cast doubt on the purity of such acetate-utilizing cultures as were available. Since Baar's original strain was impure (though his media may equally have contained some essential micronutrient of which he was unaware but which was absent from the media of subsequent workers), acceptance of the species *D. rubentschikii* should await reisolation of a new pure strain and its deposition in a recognized culture collection. Similar considerations apply to *D. rubentschikii* var. *anomalous*, which differed from *D. desulfuricans* only in being able to grow with butyric and propionic acids.

Desulforistella hydrocarbonoblastica. This organism was described by Hvid (as Hvid-Hansen, 9) but his cultures were unfortunately lost. He has been unable to reisolate the strain (N. Hvid, *personal communication*) and it has not been reported elsewhere. Though his description of the organism suggests that it was related to none so far described, it is possible that the population studied was not pure. Therefore, taxonomic recognition should await reisolation of a strain of Hvid's description and its deposition in a recognized culture collection.

"Missing" species. The barophilic organism described by ZoBell and Morita (36) was not conserved, and its classification is not clear; coccoid forms of *Desulfovibrio* species are known (Butlin et al., J. Gen. Microbiol. **3**:iii, 1949) and it may have fitted in this genus. Organisms described before 1930 were discussed critically by Baars (1).

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