Desulfovibrio vulgaris as a model microbe for the study of corrosion under sulfate-reducing conditions

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Abstract

Corrosion of iron-containing metals under sulfate-reducing conditions is an economically important problem. Microbial strains now known as *Desulfovibrio vulgaris* served as the model microbes in many of the foundational studies that developed existing models for the corrosion of iron-containing metals under sulfate-reducing conditions. Proposed mechanisms for corrosion by *D. vulgaris* include: (1) H_2 consumption to accelerate the oxidation of Fe^0 coupled to the reduction of protons to H_2; (2) production of sulfide that combines with ferrous iron to form iron sulfide coatings that promote H_2 production; (3) moribund cells release hydrogenases that catalyze Fe^0 oxidation with the production of H_2; (4) direct electron transfer from Fe^0 to cells; and (5) flavins serving as an electron shuttle for electron transfer between Fe^0 and cells. The demonstrated possibility of conducting transcriptomic and proteomic analysis of cells growing on metal surfaces suggests that similar studies on *D. vulgaris* corrosion biofilms can aid in identifying proteins that play an important role in corrosion. Tools for making targeted gene deletions in *D. vulgaris* are available for functional genetic studies. These approaches, coupled with instrumentation for the detection of low concentrations of H_2, and proven techniques for evaluating putative electron shuttle function, are expected to make it possible to determine which of the proposed mechanisms for *D. vulgaris* corrosion are most important.

Keywords: corrosion; *Desulfovibrio*; electron shuttle; extracellular electron transfer; Fe^0 oxidation; hydrogenase; hydrogen uptake; sulfate reduction; sulfide

INTRODUCTION

Understanding the mechanisms for the corrosion of metals is key to developing strategies for preventing this economically significant problem[1,2]. Following the first suggestion that microbes might be important catalysts for the corrosion of metals[3,4], a thorough analysis of the available data led to the conclusion that sulfate-reducing microorganisms play a key role in iron corrosion[5]. However, in the 1930s, *Spirillium desulfuricans* was the only microbe known to be capable of sulfate reduction[5]. The genus and species names of this and similar strains of sulfate-reducing bacteria investigated in corrosion studies have changed over time[6,7], but most are now generally recognized as strains of *Desulfovibrio vulgaris* (Table 1).

There is substantial evidence that *Desulfovibrio* species are involved in the corrosion of iron-containing metals in anaerobic environments[69,70]. *Desulfovibrio* species were abundant within the microbial community on metal surfaces exposed to oil field production waters[71,72], corroded oil pipelines[73], corroding steel

pipe carrying oily seawater[74], rust layers on steel plates immersed in seawater[75], and the inner rust layer on carbon steel[76]. *Desulfovibrio* species were recovered in culture from corrosion sites[77–80], including a *D. vulgaris* strain isolated from an oil field separator in the Gulf of Mexico that was damaged by corrosion[41]. Microbial activity on the cathodes of bioelectrochemical systems is thought to be related to microbial corrosion[81] and *Desulfovibrio* species are often enriched on cathodes from diverse microbial communities[82–84].

Several mechanisms for *D. vulgaris* corrosion of iron-containing metals have been proposed (Figure 1). These mechanisms may not be mutually exclusive. As detailed in this review, each of these models still requires rigorous examination. However, with the increasing availability of molecular tools to probe microbial activity and tools for genetic manipulation of *D. vulgaris*[85,86], it now may be the time to either eliminate or confirm some of the existing

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Table 1. Iron corrosion studies with *Desulfovibrio vulgaris*.

Year	Strain[a]	Iron source	Lactate	Mechanism[b]	Reference
1934	*Spirillum desulfuricans*	CI	+	Ha	[5]
1939	*Vibrio desulfuricans*	MS	+	N	[8]
1947	*Vibrio desulfuricans*	MS	−	N	[9]
1951	*Vibrio desulfuricans*	Armco ingot iron	+ −	Ha	[10]
1952	*Vibrio desulfuricans*	Armco ingot iron	+ −	S	[11]
1960	*D. desulphuricans* Hildenborough NCIB 8303	MS	+	Ha	[12]
1964	*D. desulphuricans* Benghazi NCIB 8401 America NCIB 8372 Teddington R NCIB 8312 Hildenborough NCIB 8303 Llanelly NCIB 8446	MS	+?	Ha	[13]
1968	*D. desulfuricans* Teddington R	MS	+	S	[14]
1968	Hildenborough NICB 8303	MS	+	Ha	[15]
1971	*D. desulfuricans* Teddington R NCIB 8312	MS	+ − (+F)	Hs	[16]
1974	Hildenborough NCIB 8303	MS	+	S	[17]
1982	Isolated from River Thames' sediment	MS (EN2)	+	N	[18]
1986	Hildenborough NCIB 8303	MS	− (+A)	Ha	[19]
1986	Marburg DSM 2119 (Postgate and Campbell)	Steel	+ − (+A)	Ha	[20]
1986	Madison	MS	− (+F)	Ha	[21]
1990	Hildenborough NCIB 8303	MS	+	Ha	[22]
1991	DSM 1744 (Postgate and Campbell)	SS (AISI 3161)	−	N	[23]
1991	Not specified	Iron (99%) SS (Fe–15Cr–10Ni)	+	Hs	[24]
1991	Not specified	SS (410)	+	S	[25]
1991	Isolated from cutting oil emulsions	CS (SAE 1020)	+	N	[26]
1992	Woolwich NCIMB 8457	MS (BS970)	+	N	[27]
1993	NCIB 8303 (Postgate and Campbell) (Hildenborough) (DSM 644)	Iron CS (SAE 1090) SS (18-8)	+	N	[28]
1994	Not specified	CS (X52)	−	N	[29]
1995	Isolated from cutting oil emulsions	MS	+	N	[30]
1995	Not specified	SS (304)	+	N	[31]
1995	ATCC 25979	SS (304)	+	N	[32]
1997	Not specified	SS (AISI 304L)	+	N	[33]
1997	Not specified	SS (316L)	+	N	[34]
1999	ATCC 29579 (Postgate and Campbell) (Hildenborough) (NCIB 8303, DSM 644)	MS (SAE 1018) SS 304	+	N	[35]
2002	LMG 7563	MS	+	N	[36]
2004	Not specified	Iron	− (+A)	D	[37]
2004	ATCC 29579	MS (1010)	+	N	[38]
2007	DSM 664	MS (BST 503-2)	+	N	[39]
2008	Hildenborough NCIMB 8303	CS (ASTM A366)	+ − (+A)	Ha	[40]
2008	Isolated from an oil field separator	MS (AISI 1018)	−	N	[41]
2008	DSMZ 644	Iron CS (ST 37) SS (304)	+	N	[42]
2010	DSMZ 644	Alloyed steel (1.4301, UNS 304)	+	N	[43]
2013	ATCC 7757 (Postgate and Campbell) (C-6, CT1, IFO 13699, NCIB 8372)	CS (C1018)	+	N	[44]
2014	ATCC 7757	CS (C1018)	+	N	[45]
2014	ATCC 7757	CS (X70)	+	N	[46]
2014	ATCC 7757	CS (API5L X-70)	+	N	[47]
2014	ATCC 7757	CS (API5L-X70)	+	N	[48]
2015	ATCC 7757	CS (C1018)	+	F	[49]
2015	ATCC 7757	SS (304)	+	F	[50]
2016	ATCC 7757	CS (C1018)	+	N	[51]
2016	ATCC 7757	CS (UNS G10100)	+	N	[52]

Table 1. (Continued).

Year	Strain[a]	Iron source	Lactate	Mechanism[b]	Reference
2016	Hildenborough DSM 644	MS (BST 503-2)	+	N	53
2017	Not specified	CI	+	N	54
2017	ATCC 7757	MS	+	N	55
2017	ATCC 7757	CS (C1018)	+	N	56
2018	ATCC 7757	CS (C1018)	+	S	57
2019	Not specified	CS (1018)	+	N	58
2019	ATCC 7757	CS (1018)	+	N	59
2019	ATCC 7757	PS (X80)	+	N	59
2020	Hildenborough	CS (1030)	+	N	60
2020	ATCC 7757	SS (2205)	+	N	61
2020	Hildenborough	CS	+	N	62
2020	ATCC 7757	CS (X65)	+	F	63
2021	ATCC 7757	GS	+	N	64
2021	ATCC 7757	SS (410, 420, 316, 2206)	+	N	65
2021	ATCC 7757	CS (C1018)	+	N	66
2021	ATCC 7757	SS (2205)	+	N	67
2021	ATCC 7757	SS (2205)	+	N	68

[a]Strains now considered to be *Desulfovibrio vulgaris* were previously designated as *Spirillium desulfuricans*, *Vibrio desulfuricans*, *Desulfovibrio desulfuricans*, and *Desulfovibrio desulphuricans*[6,7]. Therefore, microbes that were later renamed *D. vulgaris* are listed by the name designated in the original text. Only strain designations are listed for strains designated as *D. vulgaris* in the original text. Alternative designations for these strains are described in parentheses. [b]Primary corrosion mechanism discussed. Ha, abiotic H_2 production from iron; Hs, H_2 production from iron-catalyzed by FeS mineral deposits; S, sulfide promoting iron corrosion; D, direct electron transfer; F, electron transfer with a flavin shuttle; N, not applicable (the studies focused on biofilm formation, growth inhibition, corrosion inhibition, etc.). +, lactate included; −, no lactate; − (+A), no lactate but acetate added; − (+F), cells grown on fumarate; CI, cast iron; CS, carbon steel; GS, galvanized steel; MS, mild steel; PP, pipeline steel; SS, stainless steel.
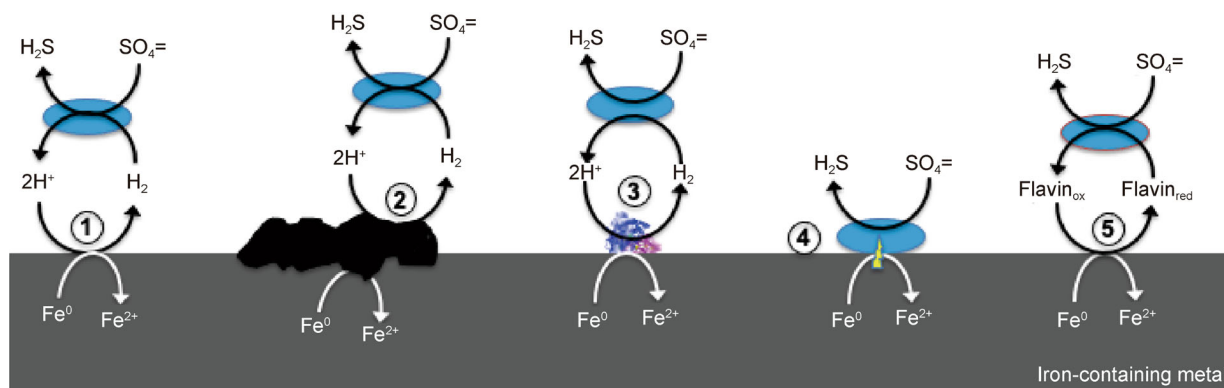

Figure 1. Previously proposed mechanisms for *Desulfovibrio vulgaris* to promote the corrosion of iron-containing metals. These include the consumption of abiotically produced H_2 (1); consumption of H_2 generated via catalysis by FeS (2) or hydrogenase (3); direct electron transfer from Fe^0 to cells via outer-surface electron transport components on the cell surface (4); and Fe^0 oxidation via reduction of the oxidized form of soluble flavin electron shuttle (Flavin$_{ox}$) with reduced flavin (Flavin$_{red}$) serving as the electron donor for sulfate reduction (5). The studies proposing these mechanisms are cited in the main text.

mechanistic models for *D. vulgaris* corrosion or to develop new models. The purpose of this review is to summarize the previously proposed routes for *Desulfovibrio* species iron corrosion and to suggest experimental approaches to further advance the understanding of corrosion by this popular model microbe.

IRON CORROSION VIA AN H_2 INTERMEDIATE

The corrosion of iron-containing metals results from the oxidation of metallic iron to ferrous iron:

$$Fe^0 \rightarrow Fe^{2+} + 2e^-. \tag{1}$$

As recognized in the early analysis of corrosion by sulfate reducers[5], protons are a likely electron acceptor for the electrons derived from Fe^0. In early studies, the product of proton reduction is often referred to as "metallic hydrogen," but in the absence of data demonstrating that this form of hydrogen exists on the surface of corroding iron or can serve as an electron donor for microbial respiration, we assume that proton reduction yields H_2, a known electron donor for diverse microbes:

$$Fe^0 + 2H^+ \rightarrow Fe^{2+} + H_2. \tag{2}$$

H_2 is an electron donor for *D. vulgaris*:

$$4H_2 + SO_4^{2-} \rightarrow S^{2-} + 4H_2O, \tag{3}$$
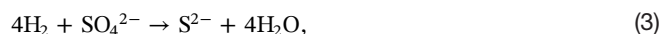
and growth on H_2 is possible if acetate is provided as a carbon source[87].

Substantial abiotic H_2 production from Fe^0 was discounted in the early version of the model in which H_2 serves as an electron carrier between Fe^0 and cells[5]. However, the mechanism by which cells promoted the oxidation of Fe^0 with the production of H_2 was not specified. It is now known that the extent of abiotic H_2 production depends upon the form of the iron-containing metal. For example, pure Fe^0 abiotically produces substantial H_2 when submerged in anoxic water at circumneutral pH whereas 316 stainless steel does not[88,89].

This difference in H_2 production between Fe^0 and stainless steel could provide one method for evaluating whether *D. vulgaris* relies on H_2 production to consume electrons from iron-containing metals. The closely related sulfate reducer *D. ferrophilus* reduced sulfate when pure Fe^0 was the electron donor, but not in a medium with stainless steel[90]. In contrast, *Geobacter* species capable of direct electron uptake could use either iron form as an electron donor[88–90]. These results indicated that *D. ferrophilus* was incapable of direct electron uptake and required the production of H_2 to mediate electron transfer between Fe^0 and cells.

The most direct approach to evaluating whether H_2 is an important intermediate in electron uptake from extracellular electron donors may be to generate a mutant that is unable to consume H_2[91]. *D. vulgaris* Hildenborough has multiple hydrogenases that have different localizations and metal constituents: the periplasmic [NiFe] HynAB-1 and HynAB-2, the periplasmic [Fe] HydAB, the periplasmic [NiFeSe] HysAB, the cytoplasmic [Fe] HydC, and the cytoplasmic membrane-bound Coo and Ech hydrogenases[92]. Deletions of genes for HydAB, HynAB-1, or HysAB negatively impacted the growth of *D. vulgaris* Hildenborough with H_2 as the electron donor[93–95]. However, these single-gene deletion mutants and a double deletion mutant of HynAB-1 and HydAB[95] still grew on H_2 as the electron donor, indicating redundant, complementary functions of the multiple hydrogenases. Thus, the construction of a strain with multiple hydrogenase gene deletions may be required to rigorously evaluate the role of H_2 in corrosion.

Transcriptomic analysis comparing growth on H_2 supplied from proton reduction with an iron electrode poised at −1.1 V versus growth on H_2 simply bubbled into medium revealed that the genes for HynAB-1 and HydAB were more highly expressed during growth on the cathodic H_2[40]. Gene transcripts for HysAB were more abundant when H_2 was bubbled into the medium. Gene deletions that prevented the function of the HynAB-1 and HydAB hydrogenases inhibited electron uptake from the iron cathodes[40], as might be expected for cathodes poised at a low potential to induce H_2 production. The impact of the hydrogenase gene deletions on corrosion of iron that was not artificially poised at a negative potential was not determined because wild-type cells could not be grown under these conditions[40]. Lack of growth on unpoised

iron suggests an inability to use Fe^0 as an electron donor. This difference between artificially poised iron cathodes and unpoised iron metal is an important consideration when evaluating other studies[19] that have concluded that H_2 is an important intermediate in iron corrosion by *D. vulgaris* based on experiments with electrochemically poised iron electrodes.

However, there is some indirect evidence for H_2 serving as an intermediary electron carrier between Fe^0 and *D. vulgaris*, especially when H_2 is not the sole electron donor. *D. vulgaris* did not reduce sulfate when steel wool was provided as the sole electron donor, but when lactate was added as an additional electron donor, more sulfide was produced than was possible from lactate oxidation alone[20]. In contrast, *D. sapovorans*, which cannot utilize H_2, did not produce substantially more sulfide when grown in the presence of lactate and steel wool, than when grown with lactate alone. These results suggested that H_2 was an intermediary electron carrier for *D. vulgaris* electron uptake from the steel wool during growth with lactate[20]. The expression of one or more uptake hydrogenases is expected to be upregulated when H_2 is serving as an electron donor[96–98]. Thus, transcriptional and/or proteomic studies may be useful in further assessing the role of H_2 as an electron donor during corrosion in the presence of lactate. Additional indirect evidence for the importance of H_2 as an electron carrier was the finding that *D. vulgaris* corroded "mild steel" faster than the gram-positive *D. orientis*, which cannot consume H_2[12,13].

Other early studies suggested that H_2 production from iron was not a mechanism for corrosion[10,11]. However, the medium for investigating the possibility for H_2 serving as an electron donor did not include acetate, which is required as a carbon source for growth on H_2. Therefore, no conclusion on the role of H_2 is possible from those studies.

FACTORS PROMOTING H_2 PRODUCTION

In a diversity of microbes, hydrogenases released from lysed cells, or specifically transported to the outer surface of living cells, facilitate the production of H_2 from Fe^0[99–102]. For example, methanogens highly effective in corrosion can produce an extracellular hydrogenase that enhances H_2 production from Fe^0[99]. Such extracellular hydrogenases have not been reported in *Desulfovibrio* species, but moribund cells of *D. vulgaris* release periplasmic hydrogenases that can retain activity for months[103]. Subjecting *D. vulgaris* to starvation, a condition likely to promote cell death and lysis, enhanced corrosion[45,58]. Therefore, studies to evaluate the role of extracellular hydrogenases in corrosion by *D. vulgaris* are warranted.

The iron sulfide that precipitates on iron-containing metals during corrosion coupled to sulfate reduction may also increase H_2 production. The addition of FeS reduced the overpotential necessary to produce H_2 from iron cathodes, suggesting a role for FeS in promoting the formation of H_2[16]. In studies in which the culture was grown on fumarate rather than via sulfate reduction, the current was generated at more

positive potentials when FeS was deposited on either mild steel or platinum cathodes[14]. These results further indicate that FeS may serve as a catalyst for H_2 generation. However, in studies with carbon steel coupons, it appeared that higher accumulations of sulfide inhibited corrosion[57]. The ability of *D. vulgaris* to corrode steel with either benzyl viologen as the electron acceptor[15] or when growing on fumarate[21] demonstrated that sulfide production was not essential for corrosion. Thus, a clear-cut concept for the role of FeS in corrosion has yet to be established.

Technology for measuring H_2 concentrations at extremely low concentrations during corrosion is available[89]. Thus, with the appropriate H_2 detector it should be possible to directly evaluate the role of FeS in facilitating H_2 production from iron-containing metals, simply by monitoring H_2 generation in the presence or absence of different quantities of FeS precipitate.

ELECTRON SHUTTLES OTHER THAN H_2

Soluble redox-active molecules promote extracellular electron exchange between microbes and minerals, electrodes, and other microbial species[104–107]. These electron shuttles typically accelerate extracellular electron exchange by alleviating the need for outer-surface electron transfer components to establish direct electrical contact with particulate extracellular donors and acceptors. The addition of riboflavin and flavin adenine dinucleotide enhanced *D. vulgaris* corrosion of carbon steel and stainless steel[49,50,63]. However, amendments of these cofactors, which are important for the function of numerous proteins, could influence *D. vulgaris* growth and metabolism in many ways. To determine whether flavins can serve as an electron shuttle for the corrosion of iron-containing metals coupled to sulfate reduction it is necessary to demonstrate that: (1) the metals are capable of reducing the flavins; and (2) that the reduced flavins can serve as electron donors for sulfate reduction.

DIRECT ELECTRON UPTAKE

Direct electron uptake from iron-containing metals has been demonstrated with *Geobacter sulfurreducens* and *Geobacter metallireducens*[88–90]. Strains unable to utilize H_2 readily reduced fumarate, nitrate, or Fe(III) with pure Fe^0 or stainless steel as the electron donor. Deletion of genes for outer-surface, multiheme *c*-type cytochromes previously shown to be involved in electron exchange with other extracellular donors/acceptors inhibited the corrosion.

There are no examples of similar studies with sulfate-reducing microorganisms. It was suggested that *c*-type cytochromes positioned in the outer membrane of *D. vulgaris* might be able to make an electrical connection with Fe^0[108]. However, subsequent studies have indicated that *D. vulgaris* does not have outer-surface cytochromes[92]. Clear next steps in this line of investigation would be to rigorously verify whether cytochromes are exposed on the outer surface of *D. vulgaris*, and if so, evaluate their role in iron corrosion

with the appropriate gene deletion studies. Genetic, biochemical, biophysical, and immunological approaches previously employed for investigating the location and function of the outer-surface cytochromes of *Geobacter* would be suitable[109–112].

Although it has been suggested that several of the *c*-type cytochromes of *D. ferrophilus* may be localized in the outer membrane, no genetic studies have been conducted to determine whether they are involved in extracellular electron exchange[90,113–115]. As noted above, experimental analysis of iron corrosion by *D. ferrophilus* has suggested that it relies on H_2 as an intermediary electron carrier rather than direct electron uptake[90].

CONCLUSIONS AND FUTURE DIRECTIONS

Sulfate-reducing microorganisms are considered to be important agents for catalyzing the corrosion of iron-containing metals and *D. vulgaris* has historically been the model microbe of choice for elucidating the mechanisms for corrosion by sulfate reducers. As summarized above (Figure 1), previous studies have suggested several mechanisms by which *D. vulgaris* may enhance corrosion, but each of the proposed mechanisms requires further experimental evaluation. The mechanisms for electron transfer between iron-containing metals and *Geobacter* species were elucidated with genome-scale transcriptomics coupled with phenotypic analysis of mutant strains in which the genes for proteins hypothesized to be involved in electron transfer were deleted[88,89]. Deletion of the genes for hydrogenases and hypothesized outer-surface electrical contacts made it possible to determine the role of H_2 as an intermediary electron carrier and to identify likely electrical contacts on the outer surface of the cell. A similar approach seems possible for the study of *D. vulgaris* corrosion mechanisms. Transcriptomics of *D. vulgaris* biofilms is possible[39,40] to aid in identifying components that may have increased expression during corrosion of iron-containing metals versus other growth modes. Other candidates for corrosion components may be identified from the known physiological roles of proteins or their cellular location. Methods for the targeted deletion of genes in *D. vulgaris* are available[85,86] making it possible to evaluate the function of proteins hypothesized to be of importance. In fact, an extensive library of *D. vulgaris* mutants is publicly available, potentially eliminating the substantial investment of time and resources required for mutant construction[86]. Comparison of corrosion capabilities with Fe^0, which readily reduces protons to generate H_2, versus stainless steel, which does not generate H_2, provides an additional tool to evaluate the role of H_2 as an intermediary electron carrier for corrosion[89,90]. Mechanisms for the corrosion of carbon steel, the most common form of iron in structural materials, should also be investigated. The hypothesis that FeS deposits stimulate H_2 production from iron-containing metals should be readily addressable with highly sensitive H_2 detection systems[88,89]. Mechanistic and genetic[116–120] approaches for the study of the role of electron shuttles in

electron transfer to minerals and electrodes should be applicable to the study of the role of flavins as electron shuttles for corrosion. Therefore, it is expected that *D. vulgaris* will continue to serve as an important model microbe for the further elucidation of mechanisms for corrosion under sulfate-reducing conditions.

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REFERENCES

1 Procópio L. The era of 'omics' technologies in the study of microbiologically influenced corrosion. *Biotechnol Lett*. 2020;42:341–56.

2 Lekbach Y, Liu T, Li Y, Moradi M, Dou W, Xu D, et al. Microbial corrosion of metals: the corrosion microbiome. *Adv Microb Physiol*. 2021;78:317–90.

3 Garrett JH. The action of water on lead, H K Lewis, London; 1891.

4 Gaines R. Bacterial activity as a corrosive influence in the soil. *J Ind Eng Chem*. 1910;2:128–30.

5 von Wolzoge Kühr CAH, van der Vlugt LS. The graphitization of cast iron as an electrobiochemical process in anaerobic soil. *Water*. 1934;18:147–65.

6 Miller JDA, Tiller AK. Microbial corrosion of buried and immersed metal. In: Miller JDA, editor. Microbial aspects of metallurgy. New York, NY: Elsevier; 1970. p. 61–105.

7 Iverson WP. Microbial corrosion of iron. In: Neilands JB, editor. Microbial iron metabolism. New York, NY: Elsevier; 1974. p. 475–513.

8 Bunker HJ. Microbiological experiments in anaerobic corrosion. *J Soc Chem Ind*. 1939;58:93–100.

9 Butlin KR, Adams ME. Autotrophic growth of sulphate-reducing bacteria. *Nature*. 1947;160:154–5.

10 Spruit CJP, Wanklyn JN. Iron/sulphide ratios in corrosion by sulphate-reducing bacteria. *Nature*. 1951;168:951–2.

11 Wanklyn JN, Spruit CJP. Influence of sulphate-reducing bacteria on the corrosion potential of iron. *Nature*. 1952;169:928–9.

12 Booth GH, Tiller AK. Polarization studies of mild steel in cultures of sulphate-reducing bacteria. *Trans Faraday Soc*. 1960;56:1689–96.

13 Booth GH. Sulphur bacteria in relation to corrosion. *J Appl Bacteriol*. 1964;27:174–81.

14 Booth GH, Elford L, Wakerley DS. Corrosion of mild steel by sulphate-reducing bacteria: an alternative mechanism. *Br Corros J*. 1968;3:242–5.

15 Booth GH, Tiller AK. Cathodic characteristics of mild steel in suspensions of sulphate-reducing bacteria. *Corros Sci*. 1968;8:583–600.

16 King RA, Miller JDA. Corrosion by the sulphate-reducing bacteria. *Nature*. 1971;233:491–2.

17 Costello JA. Cathodic depolarization by sulphate-reducing bacteria. *S Afr J Sci*. 1974;70:202–4.

18 Gaylarde CC, Johnston JM. The effect of *Vibrio anguillarum* on anaerobic metal corrosion induced by *Desulfovibrio vulgaris*. *Internat Biodet Bull*. 1982;18:111–6.

19 Pankhania IP, Moosavi AN, Hamilton WA. Utilization of cathodic hydrogen by *Desulfovibrio vulgaris* (Hildenborough). *J Gen Microbiol*. 1986;132:3357–65.

20 Cord-Ruwisch R, Widdel F. Corroding iron as a hydrogen source for sulfate reduction in growing cultures of sulfate-reducing bacteria. *Appl Microbiol Biotechnol*. 1986;25:169–74.

21 Tomei FA, Mitchell R. Development of an alternative method for studying the role of H_2-consuming bacteria in the anaerobic oxidation of iron. Proceedings of International Conference on Biologically Induced Corrosion. National Association of Corrosion Engineers, Houston, TX. 1986. p. 309–20.

22 Czechowski MH, Chatelus C, Fauque G, Libert-Coquempot MF, Lespinat PA, Berlier Y, et al. Utilization of cathodically-produced hydrogen from mild steel by *Desulfovibrio* species with different types of hydrogenases. *J Ind Microbiol*. 1990;6:227–34.

23 Benbouzld-Rollet ND, Conte M, Guezennec J, Prieur D. Monitoring of a *Vibrio natriegens* and *Desulfovibrio vulgaris* marine aerobic biofilm on a stainless steel surface in a laboratory tubular flow system. *J Appl Bacteriol*. 1991;71:244–51.

24 Newman RC, Webster BJ, Kelly RG. The electrochemistry of SRB corrosion and related inorganic phenomena. *ISIJ Int*. 1991;31:201–9.

25 Moreno DA, de Mele MFL, Ibars JR, Videla HA. Influence of microstructure on the electrochemical behavior of type 410 stainless steel in chloride media with inorganic and biogenic sulfide. *Corrosion*. 1991;47:2–9.

26 Gomez de Saravia SG, Guiamet PS, de Mele MFL, Videla HA. Biofilm effects and MIC of carbon steel in electrolytic media contaminated with microbial strains isolated from cutting-oil emulsions. *Corrosion*. 1991;47:687–92.

27 Gaylarde CC. Sulfate-reducing bacteria which do not induce accelerated corrosion. *Int Biodeterior Biodegr*. 1992;30:331–8.

28 Geiger SL, Ross TJ, Barton LL. Environmental scanning electron microscope (ESEM) evaluation of crystal and plaque formation associated with biocorrosion. *Microsc Res Tech*. 1993;25:429–33.

29 Guezennec JG. Cathodic protection and microbially induced corrosion. *Int Biodeterior Biodegr*. 1994;34:275–88.

30 Dubey RS, Namboodhiri TKG, Upadhyay SN. Microbiologically influenced corrosion of mild steel in cultures of sulphate reducing bacteria. *Indian J Chem Technol*. 1995;2:327–9.

31 Angell P, White DC. Is metabolic activity by biofilms with sulfate-reducing bacterial consortia essential for long-term propagation of pitting corrosion of stainless steel? *J Ind Microbiol*. 1995;15:329–32.

32 Angell P, Luo J-S, White DC. Microbially sustained pitting corrosion of 304 stainless steel in anaerobic seawater. *Corros Sci*. 1995;37:1085–96.

33 Gómez de Saravia SG, de Mele MFL, Videla HA, Edyvean RGJ. Bacterial biofilms on cathodically protected stainless steel. *Biofouling*. 1997;11:1–17.

34 Angell P, Machowski WJ, Paul PP, Wall CM, Lyle FF Jr. A multiple chemostat system for consortia studies on microbially influenced corrosion. *J Microbiol Methods*. 1997;30:173–8.

35 Jayaraman A, Hallock PJ, Carson RM, Lee C-C, Mansfeld FB, Wood TK. Inhibiting sulfate-reducing bacteria in biofilms on steel with antimicrobial peptides generated in situ. *Appl Microbiol Biotechnol*. 1999;52:267–75.

36 McLeod ES, MacDonald R, Brözel VS. Distribution of *Shewanella putrefaciens* and *Desulfovibrio vulgaris* in sulphidogenic biofilms of industrial cooling water systems determined by fluorescent in situ hybridisation. *Water SA*. 2002;28:123–8.

37 Dinh HT, Kuever J, Mussmann M, Hassel AW, Stratmann M, Widdel F. Iron corrosion by novel anaerobic microorganisms. *Nature*. 2004;427:829–32.

38 Zuo R, Ornek D, Syrett BC, Green RM, Hsu C-H, Mansfeld FB, et al. Inhibiting mild steel corrosion from sulfate-reducing bacteria using antimicrobial-producing biofilms in Three-Mile-Island process water. *Appl Microbiol Biotechnol*. 2004;64:275–83.

39 Zhang W, Culley DE, Nie L, Scholten JCM. Comparative transcriptome analysis of *Desulfovibrio vulgaris* grown in planktonic culture and mature biofilm on a steel surface. *Appl Microbiol Biotechnol*. 2007;76:447–57.

40 Caffrey SM, Park HS, Been J, Gordon P, Sensen CW, Voordouw G. Gene expression by the sulfate-reducing bacterium *Desulfovibrio vulgaris* Hildenborough grown on an iron electrode under cathodic protection conditions. *Appl Environ Microbiol*. 2008;74:2404–13.

41 González-Rodríguez CA, Rodríguez-Gómez FJ, Genescá-Llongueras J. The influence of *Desulfovibrio vulgaris* on the efficiency of imidazoline as a corrosion inhibitor on low-carbon steel in seawater. *Electrochim Acta*. 2008;54:86–90.

42 Stadler R, Fuerbeth W, Harneit K, Grooters M, Woelbrink M, Sand W. First evaluation of the applicability of microbial extracellular polymeric substances for corrosion protection of metal substrates. *Electrochim Acta*. 2008;54:91–9.

43 Stadler R, Wei L, Fürbeth W, Grooters M, Kuklinski A. Infuence of bacterial exopolymers on cell adhesion of *Desulfovibrio vulgaris* on

high alloyed steel: corrosion inhibition by extracellular polymeric substances (EPS). *Mater Corros*. 2010;61:1008–16.

44 Xu D, Li Y, Gu T. D-Methionine as a biofm dispersal signaling molecule enhanced tetrakis hydroxymethyl phosphonium sulfate mitigation of *Desulfovibrio vulgaris* biofilm and biocorrosion pitting. *Mater Corros*. 2013;65:837–45.

45 Xu D, Gu T. Carbon source starvation triggered more aggressive corrosion against carbon steel by the *Desulfovibrio vulgaris* biofilm. *Int Biodeter Biodegr*. 2014;91:74–81.

46 Abu Bakar A, Noor N, Yahaya N, Mohd Rasol R, Fahmy MK, Fariza SN. Disinfection of sulphate reducing bacteria using ultraviolet treatment to mitigate microbial induced corrosion. *J Biol Sci*. 2014;14:349–54.

47 Abdullah A, Yahaya N, Noor NM, Rasol RM. Microbial corrosion of API 5L X-70 carbon steel by ATCC 7757 and consortium of sulfate-reducing bacteria. *J Chem*. 2014;2014:130345–7.

48 Rasol RM, Yahaya N, Noor NM, Abdullah A, Rashid ASA. Mitigation of sulfate-reducing bacteria (SRB), *Desulfovibrio vulgaris* using low frequency ultrasound radiation. *J Corros Sci Eng*. 2014;17:1–17.

49 Li H, Xu D, Li Y, Feng H, Liu Z, Li X, et al. Extracellular electron transfer is a bottleneck in the microbiologically influenced corrosion of C1018 carbon steel by the biofilm of sulfate-reducing bacterium *Desulfovibrio vulgaris*. *PLoS One*. 2015;10:e0136183.

50 Zhang P, Xu D, Li Y, Yang K, Gu T. Electron mediators accelerate the microbiologically influenced corrosion of 304 stainless steel by the *Desulfovibrio vulgaris* biofilm. *Bioelectrochemistry*. 2015;101:14–21.

51 Li Y, Zhang P, Cai W, Rosenblatt JS, Raad II, Xu D, et al. Glyceryl trinitrate and caprylic acid for the mitigation of the *Desulfovibrio vulgaris* biofilm on C1018 carbon steel. *World J Microbiol Biotechnol*. 2016;32:23.

52 Chen Y, Torres J, Castaneda H, Ju L-K. Quantitative comparison of anaerobic pitting patterns and damage risks by chloride versus *Desulfovibrio vulgaris* using a fast pitting-characterization method. *Int Biodeterior Biodegr*. 2016;109:119–31.

53 Zhang Y, Pei G, Chen L, Zhang W. Metabolic dynamics of *Desulfovibrio vulgaris* biofilm grown on a steel surface. *Biofouling*. 2016;32:725–36.

54 Batmanghelich F, Li L, Seo Y. Influence of multispecies biofilms of *Pseudomonas aeruginosa* and *Desulfovibrio vulgaris* on the corrosion of cast iron. *Corros Sci*. 2017;121:94–104.

55 Nwankwo HU, Olasunkanmi LO, Ebenso EE. Experimental, quantum chemical and molecular dynamic simulations studies on the corrosion inhibition of mild steel by some carbazole derivatives. *Sci Rep*. 2017;7:2436.

56 Jia R, Li YD, Xu Y, Gu D. T. Mitigation of the *Desulfovibrio vulgaris* biofilm using alkyldimethylbenzylammonium chloride enhanced by D-amino acids. *Int Biodeterior Biodegr*. 2017;117:97–104.

57 Jia R, Tan JL, Jin P, Blackwood DJ, Xu D, Gu T. Effects of biogenic H2S on the microbiologically influenced corrosion of C1018 carbon steel by sulfate reducing *Desulfovibrio vulgaris* biofilm. *Corros Sci*. 2018;130:1–11.

58 Dou W, Liu J, Cai W, Wang D, Jia R, Chen S, et al. Electrochemical investigation of increased carbon steel corrosion via extracellular electron transfer by a sulfate reducing bacterium under carbon source starvation. *Corros Sci*. 2019;150:258–67.

59 Sun YP, Yang CT, Yang CG, Xu DK, Li Q, Yin L, et al. Stern–Geary constant for X80 pipeline steel in the presence of different corrosive microorganisms. *Acta Metall Sin*. 2019;32:1483–9.

60 Scarascia G, Lehmann R, Machuca LL, Morris C, Cheng KY, Kaksonen A, et al. Effect of quorum sensing on the ability of *Desulfovibrio vulgaris* to form biofilms and to biocorrode carbon steel in saline conditions. *Appl Environ Microbiol*. 2020;86:e01664–19.

61 Thuy TTT, Kannoorpatti K, Padovan A, Thennadil S. Effect of alkaline artificial seawater environment on the corrosion behaviour of duplex stainless steel 2205. *Appl Sci*. 2020;10:5043.

62 Shiibashi M, Deng X, Miran W, Okamoto A. Mechanism of anaerobic microbial corrosion suppression by mild negative cathodic polarization on carbon steel. *Environ Sci Technol Lett*. 2020;7:690–4.

63 Wang D, Liu J, Jia R, Dou W, Kumseranee S, Punpruk S, et al. Distinguishing two different microbiologically influenced corrosion (MIC) mechanisms using an electron mediator and hydrogen evolution detection. *Corros Sci*. 2020;177:108993.

64 Wang D, Unsal T, Kumseranee S, Punpruk S, Mohamed ME, Saleh MA, et al. Sulfate reducing bacterium *Desulfovibrio vulgaris* caused severe microbiologically influenced corrosion of zinc and galvanized steel. *Int Biodeterior Biodegr*. 2021;157:105160.

65 Tran TTT, Kannoorpatti K, Padovan A, Thennadil S. A study of bacteria adhesion and microbial corrosion on different stainless steels in environment containing *Desulfovibrio vulgaris*. *R Soc Open Sci*. 2021;8:201577.

66 Unsal T, Wang D, Kumseranee S, Punpruk S, Gu T. D-tyrosine enhancement of microbiocide mitigation of carbon steel corrosion by a sulfate reducing bacterium biofilm. *World J Microbiol Biotechnol*. 2021;37:103.

67 Tran TTT, Kannoorpatti K, Padovan A, Thennadil S. Effect of pH regulation by sulfate-reducing bacteria on corrosion behaviour of duplex stainless steel 2205 in acidic artificial seawater. *R Soc Open Sci*. 2021;8:200639.

68 Tran TTT, Kannoorpatti K, Padovan A, Thennadil S, Nguyen K. Microbial corrosion of DSS 2205 in an acidic chloride environment under continuous flow. *PLoS One*. 2021;16:e0251524.

69 Hamilton WA. Sulphate-reducing bacteria and anaerobic corrosion. *Ann Rev Microbiol*. 1985;39:195–217.

70 Beech IB, Sunner JA. Sulphate-reducing bacteria and their role in corrosion of ferrous materials. In: Barton LL, Hamilton WA, editors. Sulfate-reducing bacteria: environmental and engineered systems. Cambridge, UK: Cambridge University Press; 2007. p. 459–82.

71 Voordouw G, Shen Y, Harrington CS, Telang AJ, Jack TR, Westlake DWS. Quantitative reverse sample genome probing of microbial communities and its application to oil field production waters. *Appl Environ Microbiol*. 1993;59:4101–14.

72 Li XX, Yang T, Mbadinga SM, Liu JF, Yang SZ, Gu JD, et al. Responses of microbial community composition to temperature gradient and carbon steel corrosion in production water of petroleum reservoir. *Front Microbiol*. 2017;8:2379.

73 Neria-González I, Wang ET, Ramírez F, Romero JM, Hernández-Rodríguez C. Characterization of bacterial community associated to biofilms of corroded oil pipelines from the southeast of Mexico. *Anaerobe*. 2006;12:122–33.

74 Vigneron A, Alsop EB, Chambers B, Lomans BP, Head IM, Tsesmetzis N. Complementary microorganisms in highly corrosive biofilms from an offshore oil production facility. *Appl Environ Microbiol*. 2016;82:2545–54.

75 Li X, Duan J, Xiao H, Li Y, Liu H, Guan F, et al. Analysis of bacterial community composition of corroded steel immersed in Sanya and Xiamen seawaters in China via method of Illumina MiSeq sequencing. *Front Microbiol*. 2017;8:1737.

76 Zhang Y, Ma Y, Duan J, Li X, Wang J, Hou B. Analysis of marine microbial communities colonizing various metallic materials and rust layers. *Biofouling*. 2019;35:429–42.

77 Feio MJ, Beech IB, Carepo M, Lopes JM, Cheung CW, Franco R, et al. Isolation and characterisation of a novel sulphate-reducing bacterium of the *Desulfovibrio* genus. *Anaerobe*. 1998;4:117–30.

78 Miranda E, Bethencourt M, Botana FJ, Cano MJ, Sánchez-Amaya JM, Corzo A, et al. Biocorrosion of carbon steel alloys by an hydrogenotrophic sulfate-reducing bacterium *Desulfovibrio* capillatus isolated from a Mexican oil field separator. *Corros Sci*. 2006;48:2417–31.

79 Tarasov AL, Borzenkov IA. Sulfate-reducing bacteria of the genus *Desulfovibrio* from south Vietnam seacoast. *Microbiology*. 2015;84:553–60.

80 Zarasvand KA, Rai VR. Identification of the traditional and non-traditional sulfate-reducing bacteria associated with corroded ship hull. *3 Biotech*. 2016;6:197.

81 Kim BH, Lim SS, Daud WRW, Gadd GM, Chang IS. The biocathode of microbial electrochemical systems and microbially-influenced corrosion. *Bioresour Technol*. 2015;190:395–401.

82 Croese E, Pereira MA, Euverink G-JW, Stams AJM, Geelhoed JS. Analysis of the microbial community of the biocathode of a hydrogen-producing microbial electrolysis cell. *Appl Microbiol Biotechnol*. 2011;92:1083–93.

83 Pisciotta JM, Zaybak Z, Call DF, Nam J-Y, Logan BE. Enrichment of microbial electrolysis cell biocathodes from sediment microbial fuel cell bioanodes. *Appl Environ Microbiol*. 2012;78:5212–9.

84 Jafary T, Yeneneh AM, Daud WRW, Al Attar MSS, Al Masani RKM, Rupani PF. Taxonomic classification of sulphate-reducing bacteria communities attached to biocathode in hydrogen-producing microbial electrolysis cell. *Int J Environ Sci Technol*. 2021. https://doi.org/10.1007/s13762-021-03635-1

85 Keller KL, Wall JD, Chhabra S. Methods for engineering sulfate reducing bacteria of the genus *Desulfovibrio*. *Methods Enzymol*. 2011;497:503–17.

86 Wall JD, Zane GM, Juba TR, Kuehl JV, Ray J, Chhabra SR, et al. Deletion mutants, archived transposon library, and tagged protein constructs of the model sulfatereducing bacterium *Desulfovibrio vulgaris* Hildenborough. *Microbiol Resour Announc*. 2021;10:e00072–21.

87 Badziong W, Thauer RK, Zeikus JG. Isolation and characterization of *Desulfovibrio* growing on hydrogen plus sulfate as the sole energy source. *Arch Microbiol*. 1978;116:41–9.

88 Tang H-Y, Holmes DE, Ueki T, Palacios PA, Lovley DR. Iron corrosion via direct metal-microbe electron transfer. *mBio*. 2019;10:e00303–19.

89 Tang H-Y, Yang C, Ueki T, Pittman CC, Xu D, Woodard TL, et al. Stainless steel corrosion via direct iron-to-microbe electron transfer by *Geobacter* species. *ISME J*. 2021;15:3084–93.

90 Liang D, Liu X, Woodard TL, Holmes DE, Smith JA, Nevin KP, et al. Extracellular electron exchange capabilities of *Desulfovibrio ferrophilus* and *Desulfopila corrodens*. *Environ Sci Technol*. 2021;55:16195–203.

91 Lovley DR. Electrotrophy: other microbial species, iron, and electrodes as electron donors for microbial respirations. *Bioresour Technol*. 2022;345:126553.

92 Heidelberg JF, Seshadri R, Haveman SA, Hemme CL, Paulsen IT, Kolonay JF, et al. The genome sequence of the anaerobic, sulfate-reducing bacterium *Desulfovibrio vulgaris* Hildenborough. *Nat Biotechnol*. 2004;22:554–9.

93 Pohorelic BK, Voordouw JK, Lojou E, Dolla A, Harder J, Voordouw G. Effects of deletion of genes encoding Fe-only hydrogenase of *Desulfovibrio vulgaris* Hildenborough on hydrogen and lactate metabolism. *J Bacteriol*. 2002;184:679–86.

94 Goenka A, Voordouw JK, Lubitz W, Gaertner W, Voordouw G. G. Construction of a [NiFe]-hydrogenase deletion mutant of *Desulfovibrio vulgaris* Hildenborough. *Biochem Soc Trans*. 2005;33:59–60.

95 Caffrey SM, Park H-S, Voordouw JK, He Z, Zhou J, Voordouw G. Function of periplasmic hydrogenases in the sulfate-reducing bacterium *Desulfovibrio vulgaris* Hildenborough. *J Bacteriol*. 2007;189:6159–67.

96 Pereira PM, He Q, Valente FM, Xavier AV, Zhou J, Pereira IA, et al. Energy metabolism in *Desulfovibrio vulgaris* Hildenborough: insights from transcriptome analysis. *Antonie Van Leeuwenhoek*. 2008;93:347–62.

97 Clark ME, He Z, Redding AM, Joachimiak MP, Keasling JD, Zhou JZ, et al. Transcriptomic and proteomic analyses of *Desulfovibrio vulgaris* biofilms: carbon and energy flow contribute to the distinct biofilm growth state. *BMC Genomics*. 2012;13:138.

98 Zhang W, Gritsenko MA, Moore RJ, Culley DE, Nie L, Petritis K, et al. A proteomic view of *Desulfovibrio vulgaris* metabolism as determined by liquid chromatography coupled with tandem mass spectrometry. *Proteomics*. 2006;6:4286–99.

99 Tsurumaru H, Ito N, Mori K, Wakai S, Uchiyama T, Iino T, et al. An extracellular [NiFe] hydrogenase mediating iron corrosion is encoded in a genetically unstable genomic island in *Methanococcus maripaludis*. *Sci Rep*. 2018;8:1–10.

100 Deutzmann JS, Sahin M, Spormann AM. Extracellular enzymes facilitate electron uptake in biocorrosion and bioelectrosynthesis. *mBio*. 2015;6:e00496–15.

101 Philips J, Monballyu E, Georg S, De Paepe K, Prévoteau A, Rabaey K, et al. An Acetobacterium strain isolated with metallic iron as electron donor enhances iron corrosion by a similar mechanism as *Sporomusa sphaeroides*. *FEMS Microbiol Ecol*. 2019;95:fiy222.

102 Philips J. Extracellular electron uptake by acetogenic bacteria: does H_2 consumption favor the H_2 evolution reaction on a cathode or metallic iron? *Front Microbiol*. 2020;10:2997.

103 Chatelus C, Carrier P, Saignes P, Libert MF, Berlier Y, Lespinat PA, et al. Hydrogenase activity in aged, nonviable *Desulfovibrio vulgaris* cultures and its significance in anaerobic biocorrosion. *App Environ Microbio*. 1987;53:1708–10.

104 Lovley DR, Holmes DE. Electromicrobiology: the ecophysiology of phylogenetically diverse electroactive microorganisms. *Nat Rev Microbiol*. 2022;20:5–19.

105 Glasser NR, Saunders SH, Newman DK. The colorful world of extracellular electron shuttles. *Annu Rev Microbiol*. 2017;71:731–51.

106 Huang B, Gao S, Xu Z, He H, Pan X. The functional mechanisms and application of electron shuttles in extracellular electron transfer. *Curr Microbiol*. 2018;75:99–106.

107 Brutinel ED, Gralnick JA. Shuttling happens: soluble flavin mediators of extracellular electron transfer in *Shewanella*. *Appl Microbiol Biotechnol*. 2012;93:41–8.

108 Van Ommen Kloeke F, Bryant RD. Localization of cytochromes in the outer membrane of *Desulfovibrio vulgaris* (Hildenborough) and their role in anaerobic biocorrosion. *Anaerobe*. 1995;1:351–8.

109 Mehta T, Coppi MV, Childers SE, Lovley DR. Outer membrane c-type cytochromes required for Fe(III) and Mn(IV) oxide reduction in *Geobacter sulfurreducens*. *Appl Environ Microbiol*. 2005;71:8634–41.

110 Qian X, Reguera G, Mester T, Lovley DR. Evidence that OmcB and OmpB of *Geobacter sulfurreducens* are outer membrane surface proteins. *FEMS Microbiol Lett*. 2007;277:21–7.

111 Leang C, Qian X, Mester T, Lovley DR. Alignment of the c-type cytochrome OmcS along pili of *Geobacter sulfurreducens*. *Appl Environ Microbiol*. 2010;76:4080–4.

112 Inoue K, Leang C, Franks AE, Woodard TL, Nevin KP, Lovley DR. Specific localization of the c-type cytochrome OmcZ at the anode surface in current-producing biofilms of *Geobacter sulfurreducens*. *Environ Microbiol Rep*. 2011;3:211–7.

113 Deng X, Dohmae N, Nealson KH, Hashimoto K, Okamoto A. Multi-heme cytochromes provide a pathway for survival in energy-limited environments. *Sci Adv*. 2018;4:eaao5682.

114 Deng X, Okamoto A. Electrode potential dependency of single-cell activity identifies the energetics of slow microbial electron uptake process. *Front Microbiol*. 2018;9:2744.

115 Chatterjee M, Fan Y, Cao F, Jones AA, Pilloni G, Zhang X. Proteomic study of *Desulfovibrio ferrophilus* IS5 reveals overexpressed extracellular multi-heme cytochrome associated with severe microbiologically influenced corrosion. *Sci Rep*. 2021;11:15458.

116 Lovley DR, Coates JD, Blunt-Harris EL, Phillips EJP, Woodard JC. Humic substances as electron acceptors for microbial respiration. *Nature*. 1996;382:445–8.

117 Nevin KP, Lovley DR. Mechanisms for Fe(III) oxide reduction in sedimentary environments. *Geomicrobiol J*. 2002;19:141–59.

118 von Canstein H, Ogawa J, Shimizu S, Lloyd JR. Secretion of flavins by *Shewanella* species and their role in extracellular electron transfer. *Appl Environ Microbiol*. 2008;74:615–23.

119 Marsili E, Baron DB, Shikhare ID, Coursolle D, Gralnick JA, Bond DR. *Shewanella* secretes flavins that mediate extracellular electron transfer. *Proc Natl Acad Sci USA*. 2008;105:3968–73.

120 Kotloski NJ, Gralnick JA. Flavin electron shuttles dominate extracellular electron transfer by *Shewanella oneidensis*. *mBio*. 2013;4:e00553–12.

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