MICROBIOLOGY

REVIEW
Lovley, *Microbiology* 2022;168:001138
DOI 10.1099/mic.0.001138

MICROBIOLOGY SOCIETY

Microbe Profile: *Geobacter metallireducens*: a model for novel physiologies of biogeochemical and technological significance

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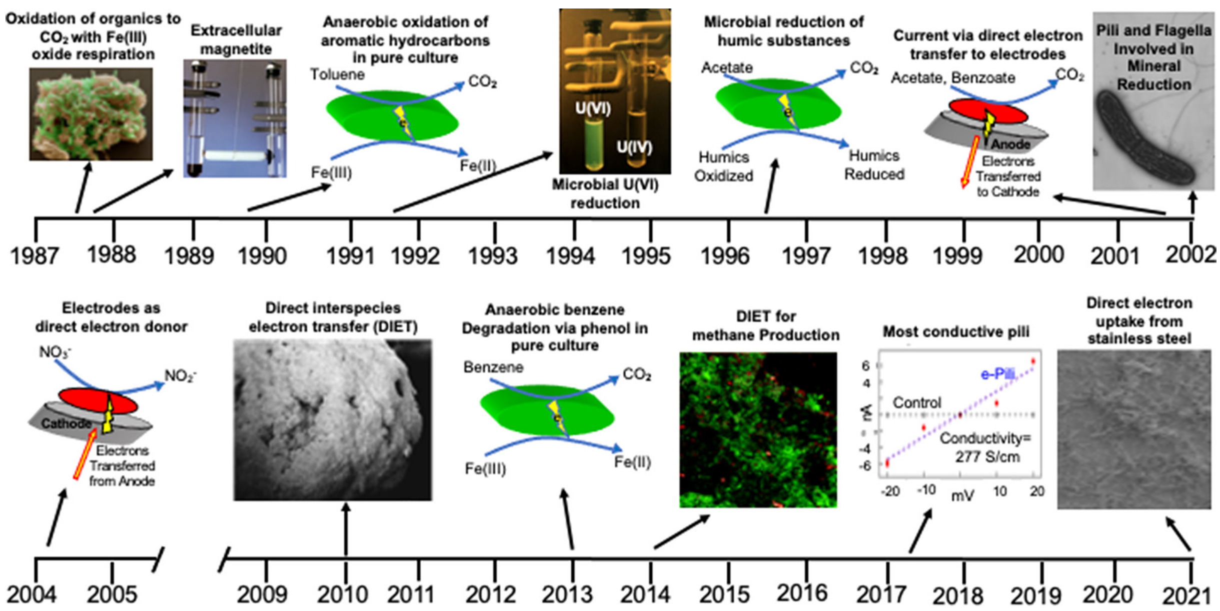

Graphical abstract

Examples of microbial physiological possibilities first discovered with *Geobacter metallireducens*.

Abstract

Geobacter metallireducens has served as the initial model for a substantial number of newly recognized microbial physiologies that play an important role in biogeochemical cycling of carbon, metals and nutrients. The strategies used by *G. metallireducens* for microbial interaction with minerals, contaminants, other microbes and electrodes have led to new technologies for bioremediation, bioenergy conversion and the sustainable production of 'green' electronics.

TAXONOMY AND PHYLOGENY

A recent phylogeny-based taxonomic revision [1] suggests the following: Class: *Desulfuromonadia*, Order: *Geobacterales*, Family: *Geobacteraceae*, Genus: *Geobacter*, Species: *metallireducens*

Received 23 August 2021; Accepted 12 January 2022; Published 16 February 2022
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Keywords: *Geobacter*; electromicrobiology; Fe(III) reduction; direct interspecies electron transfer; corrosion.
Abbreviation: DIET, direct interspecies electron transfer.

PROPERTIES

Geobacter metallireducens is a motile, nitrogen-fixing, gram-negative anaerobe that oxidizes short-chain fatty acids, alcohols and monoaromatic compounds to carbon dioxide with electron transfer to diverse extracellular electron acceptors. These acceptors include: Fe(III) and Mn(IV) oxides and metal ions (Fe^{3+}, U^{6+}, V^{5+}, Cr^{6+}, Hg^{2+}, Au^{3+}, Ag^{1+}, several ionic species of plutonium), as well as humic substances, electrodes and other microbial species. *G. metallireducens* can also conserve energy to support growth from dissimilatory reduction of nitrate to ammonia. It methylates mercury. Electrons derived from electrodes or Fe(0) support anaerobic respiration.

GENOME

The complete genome sequence of the *G. metallireducens* chromosome and its plasmid pMET1 is available, as is a genome-scale metabolic model [2].

KEY FEATURES AND DISCOVERIES

G. metallireducens (initially referred to as strain GS-15) was isolated from freshwater sediments of the Potomac River, USA (see [3, 4] for reviews of the early relevant literature). Close relatives are abundant in a diversity of anaerobic soils, aquatic sediments, subsurface environments and anaerobic digestors converting organic wastes to methane [4]. Although detailed mechanistic studies on extracellular electron transfer have primarily been conducted on its close relative *G. sulfurreducens*, *G. metallireducens* has served as the pure culture model for a substantial number of 'firsts' in microbiology.

For example, *G. metallireducens* was the first microbe found to completely oxidize organic compounds to carbon dioxide with Fe(III) or Mn(IV) oxides as the electron acceptor [4]. Fe(III) is often the most abundant potential electron acceptor for microbial respiration in soils, sediments and the subsurface, but at the time *G. metallireducens* was isolated Fe(III) reduction was thought to primarily be an abiotic redox reaction. It is now recognized that microbial oxidation of organic matter coupled to microbial Fe(III) reduction plays an important role in the global carbon cycle as well as in the release of phosphate, trace metals and metalloids that absorb to Fe(III) oxides [4]. Studies with *G. metallireducens* were the first to demonstrate that dissimilatory Fe(III) reduction could generate substantial quantities of extracellular magnetite, a mineral that serves as an indicator of microbial activity in ancient and modern sedimentary environments.

G. metallireducens was also the first microbe in pure culture found to anaerobically oxidize aromatic hydrocarbons, a type of metabolism important in the bioremediation of contaminated subsurface environments. *G. metallireducens* is an important source for biochemical studies of enzymes involved in anaerobic degradation of aromatic compounds, including a recently described megadalton complex with unprecedented redox capabilities [5]. Studies with *G. metallireducens* have revealed that it is possible for microbes to reduce highly soluble U(VI) to poorly soluble U(IV), leading to strategies for bioremediating uranium-contaminated water by stimulating *Geobacter* growth, and expanding our understanding of uranium biogeochemistry.

Studies with *G. metallireducens* were the first to demonstrate that humic substances, the most abundant form of organic matter in many soils and sediments, play a dynamic role in anaerobic microbial activity, functioning as an electron acceptor for microbial respiration and serving as an electron shuttle to promote Fe(III) oxide reduction. *G. metallireducens* was one of a cohort of closely related pure cultures that were the first microbes shown to oxidize organic compounds with direct electron transfer to electrodes. *G. metallireducens* was also the first microbe found to directly accept electrons from electrodes to support anaerobic respiration. These findings led to bioelectrochemical technologies for generating electric current from waste organic matter as well as promoting bioremediation with electrodes.

G. metallireducens was the first microbe found to make electrical connections with another microbial species to enable the anaerobic syntrophic metabolism of organic substrates. This direct interspecies electron transfer (DIET) was initially observed in a laboratory evolution experiment with *G. sulfurreducens* as the electron-accepting partner. However, *G. metallireducens* was subsequently found to make electrical connections with methanogens [6], serving as a model for DIET in the conversion of organic wastes to methane in anaerobic digesters and methane production in soils and sediments [4].

The discovery of electrically conductive pili, an important conduit for long-range extracellular electron transfer and a sustainably produced electronic material for novel electronics applications [4], stemmed from the observation that *G. metallireducens* specifically expressed pili when grown on Fe(III) and Mn(IV) oxides. The pilin gene of *G. metallireducens* yields pili with the highest conductivity of any known microbial protein filament [7].

OPEN QUESTIONS

- What is the physical arrangement of *c*-type cytochromes, conductive pili and other possible electrical contacts for extracellular electron transfer on the outer cell surface and how do they interact?

- What are the mechanisms for electron transport along electrically conductive pili of *G. metallireducens*?
- What is the role of flagella-based motility during growth in soils and sediments, and the function of flagella in establishing interspecies associations with methanogens for DIET?
- What enzyme(s) are involved in the anaerobic activation of benzene to produce phenol?
- What are the mechanisms for magnetite formation during microbial Fe(III) oxide reduction and what are the key environmental factors impacting on this process?

Funding information
This work received no specific grant from any funding agency.

Conflicts of interest
The author declares that there are no conflicts of interest.

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