REVIEW

Iron-oxidizing bacteria in marine environments: recent progresses and future directions

Hiroko Makita[1]

Abstract

Iron-oxidizing bacteria (FeOB) refers to a group of bacteria with the ability to exchange and accumulate divalent iron dissolved in water as trivalent iron inside and outside the bacterial cell. Most FeOB belong the largest bacterial phylum, *Proteobacteri*a. Within this phylum, FeOB with varying physiology with regards to their response to oxygen (obligate aerobes, facultative and obligate anaerobes) and pH optimum for proliferation (neutrophiles, moderate and extreme acidophiles) can be found. Although FeOB have been reported from a wide variety of environments, most of them have not been isolated and their biochemical characteristics remain largely unknown. This is especially true for those living in the marine realm, where the properties of FeOB was not known until the isolation of the *Zetaproteobacteria Mariprofundus ferrooxydans*, first reported in 2007. Since the proposal of *Zetaproteobacteria* by Emerson et al., the detection and isolation of those microorganisms from the marine environment has greatly escalated. Furthermore, FeOB have also recently been reported from works on ocean drilling and metal corrosion. This review aims to summarize the current state of phylogenetic and physiological diversity in marine FeOB, the significance of their roles in their environments (on both global and local scales), as well as their growing importance and applications in the industry.

Keywords Biodiversity · Biogeography · FeOB · Iron-oxidizing bacteria · Marine environments · Microbial ecology · *Zetaproteobacteria*

Introduction

Iron is one of the most common elements on Earth and the fourth most abundant element in the Earth's crust (Wedepohl 1995). Iron has a wide range of oxidation states but exists mostly in +2 or +3 states in the natural environment. The valence of iron depends on the prevailing environmental physicochemical conditions, such as pH, O_2 concentration, and redox potential. Iron occurs in many mineral phases, including (hydr)oxides, carbonates, silicates and sulfides. The oxidation of ferrous to ferric iron releases energy, which is harnessed by some iron-oxidizing prokaryotes. Ferrous iron is stable under anoxic conditions but can autoxidize in air. Some microbial communities that are unable to use solar energy via photosynthesis use energy from iron oxidation for CO_2 assimilation (Schwertmann and Cornell 2000).

Iron-oxidizing chemolithoautotrophs were first identified in the nineteenth century (Ehrenberg 1836; Winogradsky 1888). These microorganisms became important for understanding the global iron cycle (Bach and Edwards 2003) and also for industrial applications in biomining (Bacelar-Nicolau and Johnson 1999; Rohwerder et al. 2003; Rawlings and Johnson 2007). Recently, interest has grown in iron oxidation and its impacts on biogeochemical elemental cycles in acidic and circumneutral environments under micro-aerobic and anaerobic conditions (Straub et al. 1996; Emerson and Moyer 1997; Baker and Banfield 2003; Edwards et al. 2000, 2003, 2004; Hegler et al. 2012; Klueglein and Kappler 2013). There are many kinds of microorganisms that utilize iron in the marine environment which contribute to this. Among those that inhabit the ocean, most known lineages fall into one class: *Zetaproteobacteria*.

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Distribution of *Zetaproteobacteria*

All *Zetaproteobacteria* strains isolated so far originate from the marine environment (Table 1). Recent culture-dependent and -independent microbiological characterizations have revealed that a species of *Zetaproteobacteria, Mariprofundus ferrooxydans* (Emerson et al. 2007) and its relatives commonly occur in oceanic environments around the world (Table 2; Fig. 1). *Mariprofundus ferrooxydans* strains PV-1^T and JV-1 were first isolated from the Loihi seamount vent field (Emerson and Moyer 2002; Emerson et al. 2007) and classified in *Gammaproteobacteria*, but detailed phylogenetic analysis subsequently showed that they were in fact strains of the novel class now generally known as *Zetaproteobacteria* (Emerson et al. 2007). Singer et al. conducted a genomic analysis of *M. ferrooxydans* PV-1 and confirmed the presence of potential genes contributing to iron oxidation (Singer et al. 2011). The biogeographic distribution of deep-sea Zetaproteobacterial populations has been investigated in several Pacific submarine hydrothermal systems (McAllister et al. 2011) which identified 28 OTUs, some of which were endemic to a single locality, suggesting *Zetaproteobacteria* is much more diverse than expected.

Indeed, although deep-sea hydrothermal fields, particularly microbial mats and Fe-rich hydrothermally influenced sediments in relatively low-temperature areas (Laufer et al. 2017), was initially considered to be the main habitat of *Zetaproteobacteria*; recently they have been recovered from a wide range of other marine environments such as surface of shallow sediments, beach aquifer, and surface water (Table 2; Fig. 1). In addition, some *Zetaproteobacteria* members have been also found in association with metallic corrosion moiety (McBeth et al. 2011). Nevertheless, the true diversity, physiology, and ecology of *Zetaproteobacteria* (Fig. 2) still remains much unknown due to the fact that only very few strains have been isolated for further studies.

Features of *Zetaproteobacteria*

As *Zetaproteobacteria* became recognized as a cosmopolitan group, their potential significant roles in biogeochemical processes in iron-rich redox-cline environments have begun to be investigated (Emerson and Moyer 2010).

Mariprofundus ferrooxydans, the best known *Zetaproteobacteria*, is an iron-oxidizing neutrophilic chemolithoautotroph that produces helical Fe-(oxy)hydroxide "stalks" (Emerson and Moyer 2002; Emerson et al. 2007; Chan et al. 2011; Figs. 3, 4). These stalks morphologically resemble those produced by the *Betaproteobacteria* genus *Gallionella* (Ehrenberg 1836; Pringsheim 1949; Kucera and Wolfe 1957; Ghiorse 1984; Hallbeck and Pedersen 1990, 1991; Hallbeck et al. 1993; Hallberg and Ferris 2004; Hanert 2006), and as such, helical Fe-(oxy)hydroxide stalks in deep-sea hydrothermal environments were long regarded as potential products of deep-sea *Gallionella* populations (Halbach et al. 2001), until the first isolation of *M. ferrooxydans* (Emerson et al. 2007; Emerson and Moyer 2002).

Mariprofundus micogutta ET2 was recently isolated from deep-sea hydrothermal environments (Makita et al. 2017; Fig. 2), and *M. aestuarium* CP-5 *and M. ferrinatatus* CP-8 from near shore environments (Chiu et al. 2017). These three strains produce iron oxides products that are distinct in morphology from the usual stalks, with *M. micogutta* ET2 forming filamentous structures and *M. aestuarium* CP-5 and *M. ferrinatatus* CP-8 forming dread-like structures (Fig. 3e). Furthermore, the iron oxides produced by *M. aestuarium* CP-5 and *M. ferrinatatus* CP-8 are very similar to those produced by the freshwater iron oxidizing *Betaproteobacteria Ferriphaselus* sp. strain R-1 in morphology (Kato et al. 2015; Fig. 4c, d). As previously mentioned, stalks made by *M. ferrooxydans* PV-1 is also similar in morphology to those produced by *Gallionella ferruginea* (Hallbeck and Pedersen 1990). It is notable that in both cases, the laboratory culturing conditions of the relevant *Zeta-* and *Betaproteobacteria* strains were very similar. As it is difficult to precisely determine the morphology of iron oxides produced by each strain in their natural environment (due to multiple strains being present together), it is possible that they produce different iron oxides structures in nature. Taken together, these cases potentially indicate that the condition of laboratory culturing can have an determining influence on the morphological structure of iron-oxides produced.

Very recently, two strains (TAG-1 and SV-108) of a novel *Zetaproteobacteria* named *Ghiorsea bivora* were isolated (Mori et al. 2017), both strains were unique in being able to utilize either Fe(II) or molecular hydrogen (H_2) as the sole electron donor and oxygen as the terminal electron acceptor. Other known iron oxidizing bacteria thus far did not have the ability to use molecular hydrogen as the sole electron donor. Both strains precipitated iron oxides as amorphous particulates, but did not produce stalk structures which is consistent with the fact that they do not possess known putative genes for stalk-formation (xag operon) which are conserved in the genomes of several *Mariprofundus* species that do produce stalks (Kato et al. 2015). Presumably, these two strains of *G. bivora* produce a different type of exopolymer that prevents them from becoming encrusted in iron oxides, as has been proposed for several non-stalk forming freshwater FeOB (Emerson et al. 2007).

Table 1 A summary of the genome and physiological characteristics of each isolated *Zetaproteobacteria*

Name	*Ghiorsea bivora*	*Ghiorsea bivora*	*Mariprofundus aestuarium*	*Mariprofundus ferrinatatus*	*Mariprofundus ferrooxydans*	*Mariprofundus ferrooxydans*	*Mariprofundus micogutta*
Strain	TAG-1	SV-108	CP-5	CP-8	JV-1	PV-1	ET2
Type strain	Yes		Yes			Yes	Yes
Source environment	Deep-sea hydrothermal Fe mat	Deep-sea hydrothermal Fe mat	Estuarine water column	Estuarine water column	Deep-sea hydrothermal Fe mat	Deep-sea hydrothermal Fe mat	Deep-sea hydrothermal sediment
Genome size (Mbp)	2.16	2.16	2.54	2.3	2.76	2.8	2.5
GC content (%)	42.68	42.68	51	54	54	54	49
Protein count cording gene	2184	2184	2427	2237	2627	2866	2417
tRNA count	37	37	50	45	46	48	49
Cell morphology	Rod	Rod	Curved, short rod	Curved, short rod	Curved rod	Curved rod	Curved, short rod
µm	0.3×1.5–2.0	0.3×1.5–2.0	$0.43 \pm 0.05 \times 1.01 \pm 0.18$	$0.43 \pm 0.05 \times 1.01 \pm 0.18$	0.5×2.0–5.0	0.5×2.0–5.0	0.5×1.0–1.6
Doubling time (h)	21.8, 14.1*	20, 16.3*	19.5	27	12	12	24
Growth salinity (‰)	+	+	+	+	+	+	+
Range	ND*	ND	7–31.5	7–31.5	ND	3.5–35	10–40
Optimum	ND	ND	14–17.5	14–17.5	ND	28–31.5	27.5
Growth temperature (°C)							
Range	5–30	5–30	10–30	15–35	10–30	10–30	15–30
Optimum	20	20	20–25	25–30	30	30	25
Growth pH							
Range	5.5–7.5	6.0–7.5	5.5–8.3	5.5–8.3	5.5–7.2	5.5–7.2	5.8–7.0
Optimum	6.0–7.0	6.5–7.0	6.9–7.2	6.9–7.2	6.2–6.5	6.2–6.5	6.4
Energy source							
Electron acceptor	O_2	O_2	O_2	O_2	O_2	O_2	O_2
Electron donor	Fe(II), H_2	Fe(II), H_2	Fe(II)	Fe(II)	Fe(II)	Fe(II)	Fe(II)
Carbon source	CO_2	CO_2	CO_2	CO_2	CO_2	CO_2	CO_2
Iron oxides morphology	Amorphous particulates	Amorphous particulates	Dreads	Dreads	Stalk	Stalk	Filaments
Repository Accession Number	DSMZ 103937;JCM 31637; NCMA B5	NCMA B6			ATCC BAA-1021	ATCC BAA-1020	KCTC 15556; JCM 30585

Table 1 (continued)

Name	*Ghiorsea bivora*	*Ghiorsea bivora*	*Mariprofundus aestuarium*	*Mariprofundus ferrinatatus*	*Mariprofundus ferrooxydans*	*Mariprofundus ferrooxydans*	*Mariprofundus micogutta*
Reference	Mori et al. (2017)	Mori et al. (2017)	Chiu et al. (2017)	Chiu et al. (2017)	Emerson et al. (2007); Fullerton et al. (2015)	Emerson et al. (2007); Singer et al. (2011); Chiu et al. (2017)	Makita et al. (2017, 2018)

*ND No data

The iron oxides produced by *Zetaproteobacteria* can provide excellent habitational space and substrates for the microbial community, as the iron oxides structures serve as stable, porous and complex skeletons containing a variety of inorganic and organic substrates suitable for microbial growth and survival. It has been indicated that the distinctive iron oxides, such as helical twists and filaments, formation is based on association with exopolysaccarides (EPS) of cell surfaces, stalks and biofilms (Chan et al. 2009, 2011; Toner et al. 2009, 2012; Kikuchi et al. 2011, 2014; Wu et al. 2014). Although the composition and structure of EPS from *Zetaproteobacteria* is not fully understood, Chan et al. (2009) and Mitsunobu et al. (2012) suggested that the EPS was composed of acidic polysaccharide. These EPS and other organic compounds associated with the iron oxide production would serve as energy and carbon sources for mixotrophic and heterotrophic populations in iron mat microbial communities. It is likely that the chemical composition and structure of stalks produced by *Zetaproteobacteria* such as the genus *Mariprofundus* may be highly novel. A summary of genome and physiological characteristics of each *Zetaproteobacteria* strains isolated thus far is shown in Table 1.

Enrichment and isolation procedures for *Zetaproteobacteria*

Most *Zetaproteobacteria* isolated so far have been isolated by the gradient tube culture method (Emerson and Moyer 2002; Emerson and Floyd 2005), which supplies oxygen in gas phase from the top and iron from the bottom to generate a concentration gradient of the two across the medium to form a oxidation/reduction boundary region. In gradient culture, FeS or zerovalent iron is used as the iron source. The existence of a gradient allows iron oxidizing bacteria to localize in their optimum environment in the medium and grow abundantly. Therefore, it is an effective method for culturing iron oxidizing bacteria whose optimal conditions of oxygen concentration and iron concentration are difficult

to predict and prepare *a priori. Mariprofundus aestuarium* and *M. ferrinatatus* were isolated by five transplantations in gradient tubes, for example (Chiu et al. 2017). Photographs of an actual ongoing gradient culture is shown in Fig. 3.

However, an issue exists with the gradient culture method, in that agar is used to make the concentration gradient which renders counting the number of cells or examining the culture conditions difficult, when compared to using a liquid medium. Therefore, even when the initial examination of culturing conditions, accumulation of culture, and purification is carried out with a gradient medium, subsequent isolation work and experiments investigating the properties of the isolated strain is often carried out in liquid medium instead. For example, *Mariprofundus micogutta* was isolated by a serial dilution method in a liquid medium after enrichment in gradient tubes (Makita et al. 2017). *Ghiorsea bivora*, which is able to utilize Fe(II) or H_2, was also isolated in a liquid medium with zero valent iron powder by serial dilutions method in petri plates (Mori et al. 2017). Since zerovalent iron reacts with water to generate hydrogen, this method suited *G. bivora* well.

In another different method, Laufer et al. (2017) isolated a new *Zetaproteobacteria* close to *Mariprofundus* sp. M34 (98% sequence similarity) using zero-valent iron (ZVI) plates (McBeth et al. 2011; Laufer et al. 2017) with artificial seawater (ASW) medium and CO_2 as a carbon source.

Other noteworthy marine FeOB

Not all marine FeOBs are *Zetaproteobacteria*. For example, Sudek et al. (2009) reported a heterotrophic *Gammaproteobacteria* (e.g., *Pseudoalteromonas* sp. and *Pseudomonas* sp.), isolated from a volcanic seamount, with the ability to catalyze ferrous iron oxidation under micro-aerobic conditions. In addition, *Alphaproteobacteria* (e.g., *Hyphomonas* sp. from hydrothermal fields on the Juan de Fuca ridge) have been shown to oxidize Fe(II) (Edwards et al. 2003).

Table 2 Distribution of known *Zetaproteobacteria* around the world

Location name	Region	Latitude	Longitude	Setting	Isolated strain name	References
Loihi Seamount	Central Pacific	18.9500	−155.2500	Intra-plate volcano	*Mariprofundus ferrooxydans* PV-1; *Mariprofundus ferrooxydans* JV-1; *Mariprofundus* sp. M34	Moyer et al. (1994, 1995); Davis et al. (2009, 2010); Glazer and Rouxel (2009); Rassa et al. (2009); Emerson et al. (2007); Edwards et al. (2011); McAllister et al. (2011); Fleming et al. (2013); Singer et al. (2013); Fullerton et al. (2017)
Snail (Fryer)	Mariana Trough	12.9533	143.6200	Back-arc spreading center	*Ghiorsea bivora* SV-108	Kato et al. (2009a, b); Makita et al. (2016); Mori et al. (2017)
Urashima	Mariana Trough	13.51861	144.0833	Back-arc spreading center		Makita et al. (2016)
Tarama Knoll	Okinawa Trough	25.0916	124.5416	Back-arc spreading center		Makita et al. (2016)
Nagahama Bay	Satsuma Iwo-jima in the Kagoshima, Japan	30.79300	130.29600	Bay of volcanic island		Hoshino et al. (2016)
Bayonnaise knoll	Izu-Ogasawara Arc	31.95112	139.73529	Back-arc rift zone	*Mariprofundus micogutta* ET2	Makita et al. (2017)
Vailulu'u Seamount	Lau Basin	−22.2151	−176.60083	Back-arc spreading center		Staudigel et al. (2006); Sudek et al. (2009)
Tonga Arc		−24.8000	−177.0167	Arc volcano		Forget et al. (2010)
Northwest Eifuku	Mariana Arc	21.4850	144.0430	Arc volcano		Emerson and Moyer (2010); Makita et al. (2016)
Tangaroa Volcano	Kermadec Arc	−36.3250	178.0333	Arc volcano		Hodges and Olson (2009)
Clark Volcano	Kermadec Arc	−36.4490	177.8400	Arc volcano		Hodges and Olson (2009)
Franklin Seamount	Woodlark Basin	−9.9083	151.8300	Back-arc spreading center		Juniper and Fouquet (1988); Kennedy et al. (2003a, b, c)
Guaymas Basin	Gulf of California	27.00247	−111.42028	Semiclosed basins		Dhillon et al. (2003)
Juan de Fuca Ridge	North-east Pacific Ocean	45	−130.73333	Spreading center		Juniper and Fouquet (1988); Kennedy et al. (2003a, b, c); Davis et al. (2009); Orcutt et al. (2011)
East Pacific Rise	N EPR	9.8300	−104.2900	Mid-ocean ridge		Sylvan et al. (2012)
Southern Antarctic Circumpolar Current	Southern Ocean	−53.05	−46.15	between South Georgia and the South Scotia Arc		Dickinson et al. (2016)
Mid Atlantic Ridge	Atlantic Ocean	26.1820	−44.8440	ridge	*Ghiorsea bivora* TAG-1	Mori et al. (2017)
Qingdao coastal waters	China	36.51667	120.41667	Qingdao coast		Dang et al. (2011)
Southwest Indian Ridge	Indian Ridge	−38.3	51.08333	Ultraslow-spreading ridge		Cao et al. (2014)
Kebrit Deep	Northern Red Sea	24.7233	36.2767	Mid-ocean ridge		Eder et al. (2001)
Levantine basin	Eastern Mediterranean	32.93724	25.39975			Rubin-Blum et al. (2014)
Nea Kameni Island	Greece	36.39975	23.43308	Shallow embayment		Handley et al. (2010)

Table 2 (continued)

Location name	Region	Latitude	Longitude	Setting	Isolated strain name	References
Active diffuse venting hydro-thermal field	Southern Mid-Atlantic Ridge (SMAR)	13.593333	−14.51	Slow-spreading ridge		Peng et al. (2015)
Aarhus Bay	Peninsula of Jutland	56.28917	10.46807	Coast	Microaerophilic FeOx Norsminde, Microaerophilic FeOx Kalo Vig	Laufer et al. (2017)
Skagerrak	Bothnian Bay	65	23	Inside bay		Reyes et al. (2016)
Aber-Benoit	Treglonou, France	48.55334	4.535575	Tidal basin		Stauffert et al. (2013)
West Boothbay harbor	Maine, USA	43.84443	−69.64095	Shallow embayment	*Mariprofundus* sp. DIS-1	McBeth et al. (2011); Mumford et al. (2016)
Great Salt Bay	Maine, USA	44.04169	−69.53199	Salt marsh	*Mariprofundus* sp. GSB2	McBeth et al. (2011)
Cape Shores	Delaware, USA	38.78694	−75.1075	Beach aquifer		McAllister et al. (2015)
Chesapeake Bay	USA	38.9767	−76.36888	Near shore environments	*Mariprofundus aestuarium* CP-5, *Mariprofundus aestuarium* CP-8	Field et al. (2016); Chiu et al. (2017)

Recently, interesting results were obtained from culture experiments using subsurface sediment core samples obtained by International Ocean Drilling Program expeditions, for example the Gammaproteobacterial *Marinobacter* sp. (strain NP-6) with neutrophilic iron-oxidizing capabilities was isolated from aphyric, cryptocrystalline basalt over 300 m deep below the seafloor in the North Pond site of the Mid-Atlantic Ridge (Zhang et al. 2016). *In vitro* nitrogen stimulated cultivation of the same core sediments revealed, for the first time, the existence of microorganisms that grow by using basalt as the iron source. Such results indicate that iron oxidation is a key energetic process in maintaining microbial communities in subsurface basalts.

In addition, a CFB group-bacteria *Prolixibacter* sp. that oxidize zerovalent iron from crude oil was sampled from an oil well in Akita Prefecture, Japan (Iino et al. 2014, 2015). A noteworthy characteristic of this bacteria is that it can grow by oxidizing zerovalent iron in an anaerobic environment with nitrate.

Industrial applications

Iron-oxidizing bacteria (FeOB) have rich potential applications in many fields. On the seafloor, organic matter (e.g., polysaccharide) produced by FeOB are coated with iron oxides and over time these accumulate to form thick iron mats. These iron oxide structures are able to serve as a medium for the absorption of toxic trace metals, such as Mn, As, Pb, Cd, Cs and Sr (Dyer et al. 2000; Katsoyiannis and Zouboulis 2006; Pokhrel and Viraraghavan 2009; Langley et al. 2009; Sahabi et al. 2010). In fact, in municipalities that utilize groundwater extensively for daily use, such as Nara, Kyoto, Osaka and Kita-Kyushu in Japan and Haiphong City, Vietnam (Tamura et al. 1999; Thapa Chhetri et al. 2013; Yayam 2014), iron oxide-based biofiltration systems are already in use for the removal of metals such as Fe, Mn, and Al from ground water. Installation of iron oxide-based biofiltration systems by municipal water treatment facilities can lead to significant cost savings. In Jyoyo City's (Kyoto, Japan) water treatment facility, construction costs are cut by 30% compared to traditional treatment systems, chemical costs are reduced by more than 40%, and power consumption is reduced by 5% (Suzuki 2012).

Moreover, iron oxides produced by FeOB during the course of metabolism are often in the form and structure of amorphous nano-sized particles which have numerous potential industrial applications. One example is the tubular iron oxide nanoparticles produced during the growth of the freshwater iron-oxidizing betaproteobacterium *Leptothrix ochracea*. They have a unique charge–discharge property, making them a suitable material for negative electrodes in lithium ion secondary batteries (Hashimoto et al. 2014).

Fig. 1 Environments where *Zetaproteobacteria* have been detected. Deep-sea hydrothermal sediment from the NW Eifuku seamount in the North Mariana Volcanic Arc (Latitude/Longitude (L/L)=21.4850°/144.0430°, Depth:1545 m) (**a**), the Urashima site in the Mariana Trough (L/L=13.51861°/144.0833°, Depth:2930 m) (**b**), the Tarama Knoll hydrothermal field in the Okinawa Trough (L/L=25.0916°/124.5416°, Depth:1532 m) (**c**), and the Bayonnaise knoll on the Izu-Ogasawara Arc (L/L=31.95112°/139.73529°, Depth:772 m) (**d**). An overview of the Nagahama Bay at the Satsuma IWO-jima in the Kagoshima, Japan (L/L=30.7930°/130.2960°, Depth: *ca*.4 m) (**e**). Brown discoloration of seawater indicates the presence of iron oxide. Shallow hydrothermal iron-oxide deposited in Nagahama Bay (**f**). **a** and **b** are reproduces with permission from American Society for Microbiology: [*Appl Environ Microbiol*] (Makita et al. 2016). Panel **d** is reproduced with permission from Springer International Publishing AG: [*Arch Microbiol*] (Makita et al. 2017)
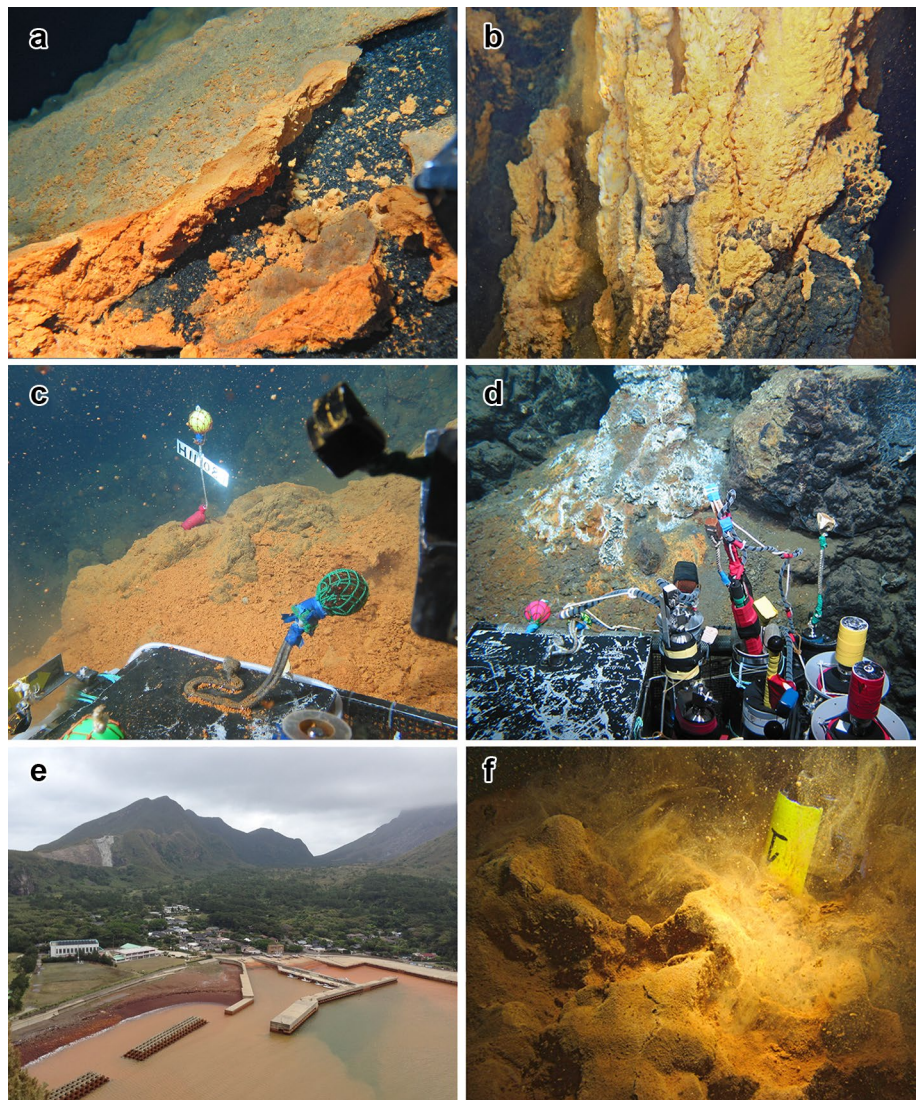
Fig. 2 Maximum-likelihood phylogenetic tree of isolated marine iron-oxidizing bacterial constructed based on the 16S rRNA gene (1349-bp). Those FeOB with limited physiological data available are excluded. Sequence similarity analysis of the 16S rRNA gene was conducted using BLAST (Altschul et al. 1997; Benson et al. 1998). The phylogenetic trees were reconstructed by the maximum-likelihood (ML) method in the MEGA 5.0 package (Tamura et al. 2011), using Jukes-Cantor model distance. Bootstrap values were calculated using 1000 replications for the ML tree. Numbers in parentheses indicate GenBank/EMBL/DDBJ database accession numbers
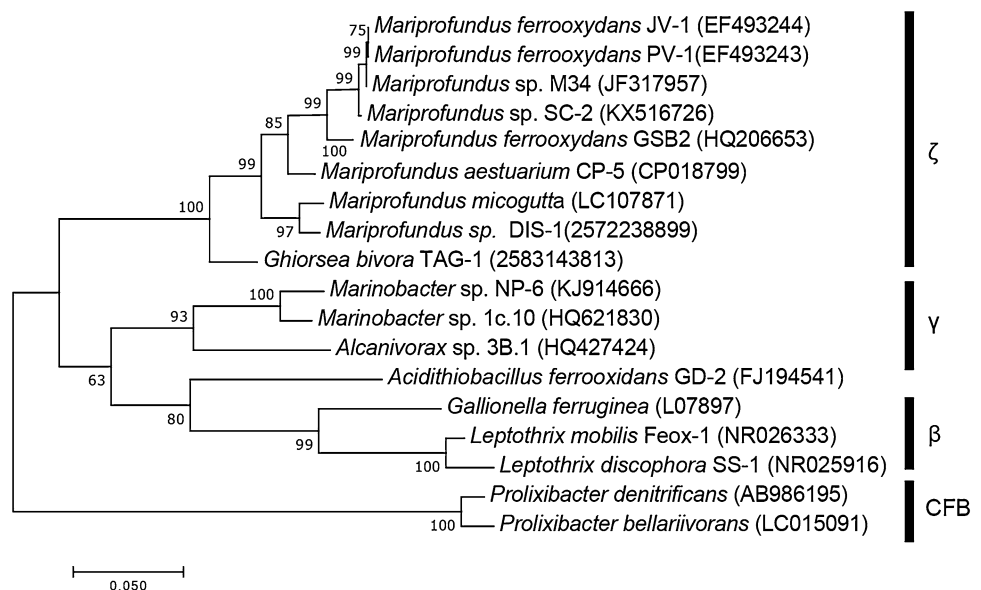
Fig. 3 *Mariprofundus* sp. culture using the gradient tube method. The state of *M. ferrooxydans* PV-1 (**a**) and *M. micogutta* ET2 (**b**) in culture with gradient medium. State of *M. aestuarium* CP-5 and *M. ferrinatatus* CP-8 on day 8 of culture in gradient medium (**c**). The orange-brown band is a colony band. Light micrographs showing cells with filamentous iron oxides produced by *M. micogutta* ET2 (**d**). Cells are DAPI stained and fluorescence images show the cells in blue. Phase contrast and fluorescence micrograph (overlay) of strain CP-5 cells (green), stained with SYBR Green I, and iron oxide dreads (**e**). Light micrographs showing *M. ferrooxydans* PV-1 cells (green), stained with Syto, attached at the end of filaments (**f**). Microscopic images of *Ghiorsea bivora* TAG-1, cells (green) were stained with SYTO13 (**g**). Scale bars indicate 10 μm (**d**), 2 μm (**e**), 5 μm (**f**), and 10 μm (**g**), respectively. Panel **a** is reproduced with permission from PLOS: [*PLoS One*] (Singer et al. 2007), panels **c** and **e** are reproduced by permission from Frontiers Media S. A.: [*Front Microbiol*] (Chiu et al. 2017), panels **b** and **d** are reproduced by permission from Springer International Publishing AG.: [*Arch Microbiol*] (Makita et al. 2017), panel **f** is reproduced by permission from PLOS: [*PLoS One*] (Emerson et al. 2007), and panel **g** is reprinted by permission from Macmillan Publishers Ltd: [*ISME Journal*] (Mori et al. 2017)
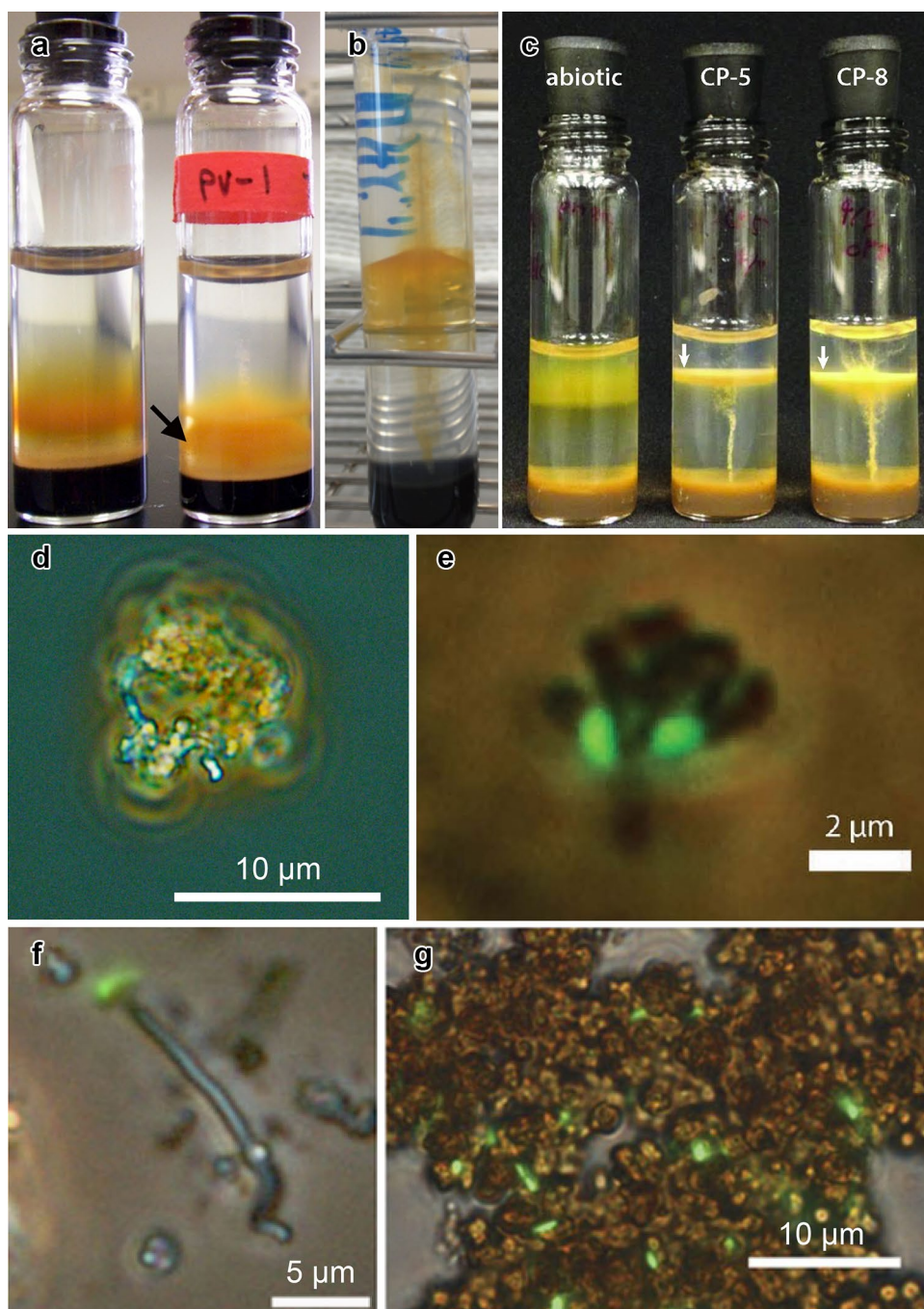
Another example is the iron oxide produced by *M. ferrooxydans* which has applications as novel multifunctional drug carriers for triggered therapeutics release as well as cancer hyperthermia applications (Kumeria et al. 2016). In addition, iron oxides of *Mariprofundus* sp. processed at 800 °C were the most optimal for photocatalytic applications the degradation rhodamine B (Wang et al. 2016).

Extracellular polysaccharide (EPS) of FeOB, which are supports of iron oxide, also have potential industrial applications. Although the chemical composition, structure, and mechanism of production of EPS from *Zetaproteobacteria* are not entirely known, the chemical composition and structure of the extra-cellular sheath produced by the iron-oxidizing *Betaproteobacteria Leptothrix cholodnii* has been elucidated (Emerson and Ghiorse 1993; Takeda et al. 2005; Makita et al. 2006). The 2-(cysteinyl)amido-2-deoxy-D-galacturonic acid residue connecting the main hetero-polysaccharide chain to the peptide side chain exhibits a novel structure (Makita et al. 2006). While the details of EPS remain largely unknown for most FeOB, these potentially
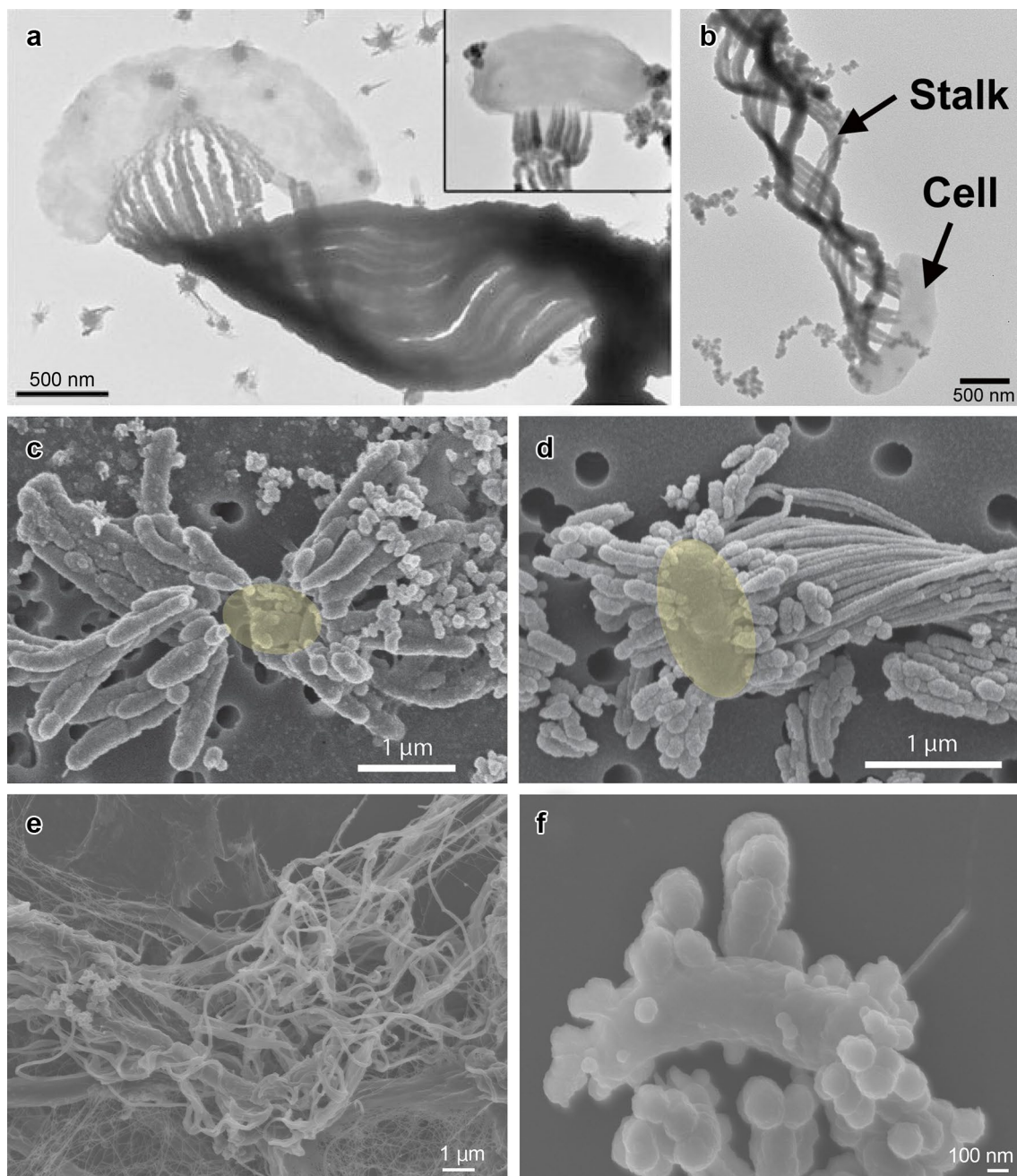
Fig. 4 Transmission electron microscope (TEM) images of *M. ferrooxydans*'s cell with stalk (**a**), (**b**). Inset: smaller cell and stalk, displayed at the same scale showing that smaller cells produce narrower stalks with fewer filaments (**a**). Scanning electron micrographs (SEM) of dreads produced by the strain CP-8, with the likely location of a missing cell denoted by a yellow oval (**c**). Dreads surrounding a freshwater betaproteobacterial FeOB *Ferriphaselus* sp. strain R-1 cell, highlighted in yellow (**d**). SEM micrograph showing the cell and extracellular materials of *M. micogutta* ET2 (**e**), and filamentous iron oxides (**f**). Scale bars: 500 nm (**a**), (**b**), 1 μm (**c**), (**d**), 100 nm (**e**) and 1 μm (**f**), respectively. Panel **a** is reproduced with permission from Macmillan Publishers Ltd: [*ISME Journal*] (Chan et al. 2011), panel **b** is reproduced with permission from PLOS: [*PLoS One*] (Singer et al. 2007), panels **c** and **d** are reproduced with permission from Frontiers Media S. A.: [*Front Microbiol*] (Chiu et al. 2017), and panels **e** and **f** are reproduced with permission from Springer International Publishing AG.: [*Arch Microbiol*] (Makita et al. 2017)

novel structures may be useful for the pharmaceutical and textile industries. For instance, moisturizing agent derived from a polysaccharide produced by *Alcaligenes latus* absorbs 1000 times its own weight in water, which can be used as medicament and cosmetics (Kurane et al. 1994). Recently, *M. ferrooxydans* has been successfully cultivated using

electric energy (Mogi et al. 2013; Summers et al. 2013). This indicates *M. ferrooxydans* exhibits inter-membrane electron transfer mechanisms from outside its cell. This electrochemical culture method may allow a continuous production of organic macromolecules from iron oxidizing bacteria for use in industry. In this way, FeOB have attractive potential applications in producing organic matter from carbon dioxide.

Furthermore, the study of the interaction between FeOB and solid-phase iron (e.g., iron in reinforced concrete) is industrially important. FeOB that grow by oxidizing zerovalent iron, such as the aforementioned CFB group-bacteria, *Prolixibacter denitrificans* and *P. bellariivorans* (Iino et al. 2014, 2015), are the source of microbial induced corrosion (MIC) of industrial products which a major issue limiting the lifespan of such products (Javaherdashti 2008). Although zerovalent iron does not exist in the natural environment, it is widely used in industrial products. Future researches on such bacteria that play a role in MIC is expected to yield effective counter-measures for this issue.

Conclusion

Until the last decade, marine FeOB were not recognized as significant players in *in-situ* ecosystems in marine environments. Although their existence and importance in the carbon cycle were predicted, few species could be isolated. However, in recent years, studies on the isolation and identification of FeOB inhabiting marine environments have been rapidly increasing (Emerson et al. 2007; Chiu et al. 2017; Laufer et al. 2017; Makita et al. 2017; Mori et al. 2017), with the number of successful isolations likely to increase with time. It is thought that FeOB play an important role in iron and carbon circulation in the ocean as it utilizes iron and CO_2 in the seawater. Although the biogeochemical iron cycle is unable to function independently from the carbon cycle, a relatively small amount of carbon is sufficient to drive and maintain it. Further investigation into the role of FeOB in CO_2 fixation in the marine environment will contribute to the understanding of the overall global carbon cycle. Furthermore, knowledge of the mechanism and total amount of CO_2 fixation by FeOB can also lead to industrially applicable methods for immobilizing CO_2 to help mitigate the effects of climate change. For that, the identification of enzymes involved in iron oxidation and using such enzymes as biomarkers to reveal the true global distribution of FeOB will be key.

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