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The *Shewanella* genus: ubiquitous organisms sustaining and preserving aquatic ecosystems.

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This review discusses the diversity among the aquatic ubiquitous γ -proteobacterial *Shewanella* genus, which acts on several cycles of Matter and forms biological interactions with both prokaryotes and eukaryotes, in addition to being implicated in ecosystem resilience and biotechnological applications.

Abstract

The Gram-negative *Shewanella* bacterial genus currently includes about 70 species of mostly aquatic γ -proteobacteria, which were isolated around the globe in a multitude of environments such as surface freshwater and the deepest marine trenches. Their survival in such a wide range of ecological niches is due to their impressive physiological and respiratory versatility. Some strains are among the organisms with the highest number of respiratory systems, depending on a complex and rich metabolic network. Implicated in the recycling of organic and inorganic matter, they are important components of organism-rich oxic/anoxic interfaces, but they also belong to the microflora of a broad group of eukaryotes from metazoans to green algae. Examples of long-term biological interactions like mutualism or pathogeny have been described, although molecular determinants of such symbioses are still poorly understood. Some of these bacteria are key organisms for various biotechnological applications, especially the bioremediation of hydrocarbons and metallic pollutants. The natural ability of these prokaryotes to thrive and detoxify deleterious compounds explains their use in wastewater treatment, their use in energy generation by microbial fuel cells, and their importance for resilience of aquatic ecosystems.

Introduction.

In 1931, a bacterium was isolated from tainted Canadian butter (Derby and Hammer 1931). This strain, first described as belonging to the *Achromobacter* genus, was reclassified half a century later in the newly created *Shewanella* genus (MacDonell and Colwell 1985), which currently contains about 70 species listed in the list of prokaryotic names with standings in nomenclature (LPSN) database, among which more than 30 genomes are available (Euzéby 1997; Parte 2014, 2018).

The versatility of *Shewanella* physiology allows for impressive distribution of these prokaryotes, which live in a wide range of ecological niches. Strains have been isolated from the polar circles to equatorial areas, from fresh to hypersaline waters, from the surface to the deepest sediment ever studied, in pristine and polluted environments (Fig. 1) (Nealson and Scott 2006; Hau and Gralnick 2007). Probably ancestrally living in hydrothermal vents, these bacteria became ubiquitous in aquatic environments thanks to their adaptation to diverse stresses. Specific metabolic features allow them to perfectly fit into redox stratified environments, from which many species were isolated.

In addition to the metabolic versatility, this genus also contains strains resistant to a wide range of toxic compounds, enabling survival in polluted areas and the colonisation of synthetic biotopes. Furthermore, some of these bacteria actively attenuate the harmfulness of toxic products, enhancing both ecosystem resistance and resilience towards pollution. This feature, combined with the non-pathogenic behaviour of most strains, increases the interest in the genus for bioremediation applications. However, depollution is not the sole biotechnological application of *Shewanella* species since they are perfectly suitable in probiotics, protein or compound production, as well as energy generation in microbial fuel cells.

Numerous studies have highlighted the existence of biological interactions implicating *Shewanella* species and members of various phyla of eukaryotes. Indeed, these bacteria are common members of the microflora of diverse metazoans (e.g. fishes or arthropods), alveolates (e.g. brown algae) and *Plantae* (e.g. red or green algae). Furthermore, specific mutualistic and host-pathogen interactions involving *Shewanella* species have also been described, even though the identification of molecular determinants of these symbioses is still lacking.

This review aims to present up-to-date information on the *Shewanella* genus. The description of the distribution and physiological diversity of the genus, previously reviewed about ten years ago (Nealson and Scott 2006; Hau and Gralnick 2007; Fredrickson *et al.* 2008), has been amended on the basis of work from the last decade, which has provided a deeper explanation of this versatility. This review emphasises and describes the wide range of ecological niches occupied by *Shewanella* strains and their relationships with other organisms, which largely depend on their physiological versatility. The state-of-the-art in biotechnological applications implicating *Shewanella* species is also presented and discussed.

Distribution

Shewanella species are known to be ubiquitous in marine environments (Fig. 1); they can be found in every ocean. Some strains have been isolated in particular geographic areas, suggesting a putative specificity, while for some species, isolates come from very distant zones. For example, *S. algae*, originally isolated in Japanese coasts, has also been found on both sides of the North Atlantic Ocean (Simidu *et al.* 1990; Richards *et al.* 2008; Aigle, Michotey and Bonin 2015). Bacteria like *S. algae*, which comes from surface or shallow waters, could easily disperse through the flow of water, colonizing new areas, and could propagate as contaminants of ballast of cargo boats, rich in microorganisms (Brinkmeyer 2016, Dann *et al.* 2019).

Shewanella species have been isolated from nearly all depths of the marine water column, as well as intertidal zones, estuaries, and sediments from shallow areas to the deepest parts of the ocean (the Challenger Deep in the Marianna Trench) (Kato *et al.* 1998; Venkateswaran *et al.* 1998; Miyazaki *et al.* 2006; Freese *et al.* 2009; Lauro *et al.* 2013; Deng *et al.* 2014; Aigle, Michotey and Bonin 2015). Members of this genus were collected in microbial mats near hydrothermal vents (Gao *et al.* 2006). Some species have managed to colonise brackish and freshwater environments (Venkateswaran *et al.* 1999; Li *et al.* 2014; Esteve, Merchán and Alcaide 2017).

The wide distribution of the *Shewanella* genus requires the versatility and adaptability of these organisms. In order to thrive in the average coldness of the oceanic environment, these bacteria had to develop resistance mechanisms to allow for optimal growth at low temperature (Hau and Gralnick 2007). This includes the production of short and unsaturated fatty acids, such as eicosapentaenoic acid, which ensure fluidity of lipidic membranes (Denich *et al.* 2003; Abboud *et al.* 2005; Kawamoto *et al.* 2009), the production of proteins containing statistically smaller amino-acids for protein flexibility (Zhao *et al.* 2010; Banerjee and Mukhopadhyay 2012), and the involvement of chaperons or co-chaperons (Fujii, Nakasone and Horikoshi 1999; Maillot *et al.* 2019), or DNA protection systems (Yang *et al.* 2017). Finally, some polar species produce external ice-binding proteins, preventing ice crystal formation (Vance, Graham and Davies 2018; Delesky *et al.* 2019). The authors hypothesised that these proteins could inhibit freezing of the medium, and thus allow movement of the microbes through the ice layer. Albeit still poorly determined, some of these mechanisms are thought to also be implicated in hydrostatic pressure resistance since the few described piezotolerant and piezophile species are also psychrophiles (Kato *et al.* 1998; Denich *et al.* 2003; Kawamoto *et al.* 2009; Lauro *et al.* 2013; Yang *et al.* 2017). However, the psychro/piezotolerance correlation could also simply be due to the average low temperature of deep-sea water, even if both stresses increase the stiffness of biological structures.

Many described species exhibit an optimal temperature for growth below 20 °C, but the genus also contains mesophilic organisms and even some species that maintain robust growth at temperatures above 40 °C (Gao *et al.* 2006; Chang *et al.* 2008; Lemaire *et al.* 2019). As for psychrotolerance, the mechanisms allowing the preference for higher temperatures are not fully understood. The lipids and proteins of these species have compositions that increase stiffness. It has been established that chaperone proteins like HtpG are involved in survival against heat shock stress in *Shewanella* species (García-Descalzo *et al.* 2011; Honoré, Méjean and Genest 2017, Honoré *et al.* 2019). The preference for elevated temperatures allows these bacteria to proliferate near hydrothermal vents as well as surface or intertidal warm waters.

Since most of the strains have been isolated from marine environments, they are moderate halophiles, with optimal growth in the presence of about 3% dissolved salts. Nevertheless, as for temperature, some isolates exhibit higher growth rates in brackish or freshwaters or in the presence of higher salinity, allowing for colonisation of other ecological niches (Gu and Mitchell 2002; Pinhassi and Berman 2003; Borsodi *et al.* 2007; Hau and Gralnick 2007; Li *et al.* 2014; Dailey *et al.* 2016; Díaz-Cárdenas *et al.* 2017; Esteve, Merchán and Alcaide 2017; Vaidya, Dev and Sourirajan 2018).

If the *Shewanella* genus is currently present in all aquatic environments, its history should have started at the bottom of the ocean. Analysis of the available genomic data of the genus carried out by Zhong *et al.* (2018), revealed interesting data on the theoretical genome of the ancestral *Shewanella*, the closer currently described species putatively being *S. loihica* PV-4. This species was isolated from a hydrothermal venting area and is able to grow from 4 to 42 °C (Gao *et al.* 2006). Assuming that the ancestor of *Shewanella* species experienced similar living conditions, authors have proposed the evolution of the genus from this ancestor to the Na⁺-dependent psychrotolerant and mesophilic sub-groups pointed by different studies (Kato and Nogi, 2001; Zhao *et al.* 2010; Banerjee and Mukhopadhyay, 2012). Some of the Na⁺-independent marine bacteria episodically colonised freshwater environments. This speculation still has to be ascertained by physiological or biochemical studies of the concerned strains but is supported by several results. For example, the model strain *S. oneidensis* MR-1 was isolated from sediment of the Oneida freshwater lake in New York state, USA. However, due to salinity requirements, the flagellar motor composition and metagenomics data from the nearby Sargasso Sea, it is believed that the strain originated from the Atlantic Ocean and later contaminated the Oneida

Lake (Nealson, Myers and Wimpee 1991; Venkateswaran *et al.* 1999; Heidelberg *et al.* 2002; Venter *et al.* 2004; Liu *et al.* 2005; Hau and Gralnick 2007; Paulick *et al.* 2009). Similar contamination could explain the presence of *Shewanella* species in the Sea of Galilee (Lake Tiberias), a slightly saline environment in the Middle East (Mazor and Mero 1969; Pinhassi and Berman 2003). Furthermore, in most cases the freshwater isolates are sub-species of marine species and not specific lineages, which, again, supports the scenario of episodic and recent adaptation of marine species (Pinhassi and Berman 2003; Dailey *et al.* 2016).

Ecological niches

Carbon and energy metabolism: Consequences on ecological niches

The *Shewanella* genus is described as a group of heterotrophic, facultative aerobic, γ -proteobacteria that survive in oxygenated environments using dioxygen as an electron acceptor (Fig. 2) (Fu *et al.* 2014; Le Laz *et al.* 2014, 2016). Several oxidases have been described as being present in *Shewanella* species. However, it has been shown that the very efficient type A oxidase, albeit encoded in the genome of *Shewanella* species, is not produced under standard conditions in *S. oneidensis* MR-1 and so does not participate in dioxygen reduction (Le Laz *et al.* 2014, 2016). Therefore, this organism would be outcompeted in highly oxygenated environments against type A oxidase-producing organisms (Zhou *et al.* 2013). Extended to other species, this could explain why these bacteria are mainly found in anaerobic waters and sediments and only episodically in the oxic upper surface (Nealson and Scott 2006; Hau and Gralnick 2007; Fredrickson *et al.* 2008). For *Shewanella* species, a way to survive in unfavourable oxygen-rich environments is to form specific microaerobic niches, such as aggregates, marine snow, flocculates or floating biofilms (McLean *et al.* 2008; Armitano, Méjean and Jourlin-Castelli 2013; Gambari *et al.* 2018; Boeuf *et al.* 2019). In addition to the more classic sediment mixing effect on water flow, these features could explain the episodic presence of the genus in the oxygenated upper layer of water.

The genus mostly contains non-fermentative bacteria (Xu *et al.* 2005; Zhao *et al.* 2005; Nealson and Scott 2006; Hau and Gralnick 2007; Hunt *et al.* 2010; Pinchuk *et al.* 2011; Wang and Sun 2016). For a few species, it has been shown that fermentation occurs and allows bacterial survival but not growth (Pinchuk *et al.* 2011; Kane *et al.* 2016). This inability to use fermentation impairs the colonisation of strictly anoxic niches by the genus, in which it will be outcompeted by fermentative, sulphate reducing, acetogenic, or methanogenic organisms.

Unable to compete in both aerobic and anaerobic environments, the redox stratified zones form the ideal transition and many *Shewanella* isolates originate from these environments (Hau and Gralnick, 2007). Microaerobic conditions are favourable to these bacteria, they act on the degradation of organic matter and impact various cycles of matter due to their versatile respiratory network. The genus was shown to be implicated in the degradation of micro- and macroorganisms (Dos Santos *et al.* 1998; Nealson and Scott 2006; Richards *et al.* 2008; Kakizaki *et al.* 2009; Skrlin *et al.* 2011; Janda and Abbott 2014; Petit *et al.* 2015; Martin *et al.* 2015; Jie *et al.* 2018; Yagi *et al.* 2018). Organic matter degradation provides formate, lactate or pyruvate, simple or complex sugars, fatty acids, nucleosides, amino acids, osmolytes or more exotic organic compounds that are all used as carbon, nitrogen, and phosphorus sources but also to sustain a diversified and adaptable respiratory network (Fig. 2) (Nealson and Scott 2006; Driscoll *et al.* 2007; Hau and Gralnick 2007; Fredrickson *et al.* 2008; Pinchuk *et al.* 2008; Hassanshahian 2014; Wang and Sun 2016).

Shewanella species are characterised by their ability to use a wide range of electron acceptors for quinol pool oxidation and energy generation, which is summarised in Fig. 2 and reviewed elsewhere (Nealson and Scott 2006; Hau and Gralnick 2007; Fredrickson *et al.* 2008; Beblawy *et al.* 2018). However, caution has to be taken because the majority of the knowledge that has been gathered on *Shewanella* respiration comes from data obtained on the model *S. oneidensis* MR-1. In particular, the range includes oxygen, compounds belonging to the nitrogen and sulphur cycles of matter, fumarate, arsenate, trimethylamine oxide (TMAO), dimethylsulphoxide (DMSO), urocanate and various metals or metalloids (Fig. 2). For a given substrate, different respiratory complexes can be used according to the conditions or species. The case of oxygen is discussed above, but nitrate reduction exhibits a similar mechanism implicating periplasmic nitrate reductase (Nap) in most species or membranous nitrate reductase (Nar systems) in those experiencing higher concentrations of nitrate (Krause and Nealson 1997; Makemson *et al.* 1997; Zhao *et al.* 2005, 2006; Simpson, Richardson and Codd 2010). Similarly, nitrite can be reduced into ammonia by nitrite reductase or to N₂ by denitrifying *Shewanella* species. (Krause and Nealson 1997; Zhao *et al.* 2006; Youngblut *et al.* 2012; Chen and Strous 2013; Deng *et al.* 2014;). Most of the species have a highly efficient TMAO reductase system, allowing for robust growth on this substrate, which is an important osmolyte present at high concentrations in numerous eukaryotes, thus being an important substrate for organism that recycle organic matter (Dos Santos *et al.* 1998; Yancey *et al.* 2014; Lemaire *et al.* 2016, 2018). However, one of the hallmarks of this genus is the external electron transfers (EET), which is an uncommon feature in prokaryotes, making *Shewanella* species key players in metal oxidoreduction cycles and allowing for their survival in metal-rich environments (Nealson and Scott 2006; Hau and Gralnick 2007; Ha *et al.* 2017; Conley *et al.* 2018; Light *et al.* 2018; Zou *et al.* 2018, Laso-Pérez *et al.* 2019).

The mechanism of EET has been extensively studied and is currently well described, as recently reviewed by Beblawy *et al.* (2018). The process schematised in Fig. 3 is mediated by a complex assembly of *c*-type cytochromes that transfer electrons from the quinol pool to the outer face of the outer membrane. EET can be mediated by two similar outer membrane complexes: the metal-reducing systems MtrCAB and MtrDEF (Fig. 2 and 3A). Nevertheless, MtrCAB alone appears to physiologically act according to deletion experiments (Coursolle and Gralnick 2010; Schicklberger, Sturm and Gescher 2013; Beblawy *et al.* 2018). Both assemblies are composed of two decahaem *c*-type cytochromes associated with the outer membranes and a transmembrane β -barrel protein, forming a channel across the outer membrane (Fig. 3A) (White *et al.* 2013). The cytochromes are each oriented towards a different side of the membrane, making contact through the transmembrane channel (Fig. 3A). Another decahaem cytochrome, the outer membrane cytochrome OmcA, is closely related to MtrC and appears to play a similar role with the MtrAB subunits. For EET, the outer cytochrome receives electrons from its periplasmic counterpart, which oxidises a reduced periplasmic cytochrome. Several interchangeable periplasmic electron carriers, like the fumarate reductase FccA or the small tetrahaem cytochrome STC have been shown to be involved in the EET pathway, all reduced by the central quinol oxidase CymA (Fig. 3A).

EET can be performed in the following three ways: direct contact, distant contact, or mediated by external soluble electron carriers (Fig. 3B) (Beblawy *et al.* 2018). When direct contact between cells and metallic acceptors occurs, the electron transfer is performed from the external face of the outer membrane. However, when electron acceptors are scarce, the outer membrane undergoes dynamical structural rearrangements, forming outer membrane extensions called nanowires (Fig. 3B) (Beblawy *et al.* 2018; Creasey *et al.* 2018; Subramanian *et al.* 2018; Chong *et al.* 2019). These allow for contact, and thus electron transfer, with electron acceptors that are far away from the cell. These structures are thought to be important for bacterial metal reduction in biofilms, in which the upper-layer organisms cannot be in direct contact with the electron acceptor and, thus, depend on distant reduction mechanisms. Finally, if the secreted soluble electron carriers (e.g. flavins) are considered as important cofactors of the external metal reducing systems, they also could serve as external electron shuttles in the external media (Fig. 3) (Edwards *et al.* 2015; Beblawy *et al.* 2018). The presence of external flavins only occurs at high bacterial concentrations, such as in laboratory batch cultures. However, data to decipher if the flavin concentrations in physiological biofilms could be sufficient to reproduce the same process and, thus, if the mediator-based distant reduction is a physiological mechanism or a laboratory artefact, are still missing.

Biological interactions

In ecosystems, a plethora of organisms coexist. Numerous studies have highlighted the presence of *Shewanella* species living in direct contact with organisms from different domains of life (Fig. 4). *Shewanella* species can be microbionts or epibionts but also putative partners of more specific and long-term interactions. In this review, interactions will be all considered as symbiotic, regardless of beneficial or deleterious role of the bacteria on the organisms.

Metazoan

Several examples of realistic symbioses involving *Shewanella* species and metazoans have been reported. The case of *Shewanella colweliana* is one of the most fully described. This strain has been isolated from holding tanks and adult *Crassostrea virginica*, the Eastern Oyster (Weiner, Segall and Colwell 1985). Biofilms formed by the bacterium enhance settlement of the planktonic larvae of the oyster. This process is mediated by bacterial production of exopolysaccharide and melanin precursors (Fuqua and Weiner 1993; Mitra, Gachhui and Mukherjee 2015). Thus, it is thought that larvae get a selective advantage, such as protection from oxidative stress induced by UV from sunlight (Vijayan *et al.* 2017). Similar behaviours have been identified with larvae of other organisms, such as mussels or sea urchins (Huggett *et al.* 2006; Yang *et al.* 2013). After settling, bacteria can be sustained by the metazoan wastes or by colonisation of the intestinal track of the organisms, consistent with the notion that *S. colweliana* is also found in adult oysters (King *et al.* 2012).

Studies have highlighted that eukaryotes can actively promote bacterial biofilm formation for their protection. Indeed, embedded bacteria can produce compounds that are favourable for the host or toxic for parasites or predators (Penesyan, Kjelleberg and Egan 2010). Tetrodotoxin, a highly efficient neurotoxin is a noteworthy example that can be synthesised by some *Shewanella* species (Simidu *et al.* 1990; Magarlamov, Melnikova and Chernyshev 2017). This toxin can be found in various metazoan, e.g. fishes, molluscs, echinoderms, arthropods, amphibians, and flat and ribbon worms, and is thought to be acquired by the alimentation, beginning from bacteria (Itoi *et al.* 2018). It is then probable that eukaryotes inhabit or sustain the biofilms that contain *Shewanella* species in order to be protected by the accumulation of the bacterial toxin.

In this line of thought, a putative mutualistic symbiosis has been described between the strain *S. pealeana* and the longfin inshore squid *Loligo pealeii*. The bacterium was isolated from samples of the accessory nidamental gland of the mollusc, a bacteria-rich gland implicated in the final step of egg development (Bloodgood 1977; Leonardo *et al.* 1999). In exchange for the protected ecological niche, bacteria living in this organ are suspected to act on the protection of the squid eggs against abiotic stresses, pathogens, predators, and parasites (Barbieri *et al.* 1997). This is not the only cephalopod with which *Shewanella* is suspected of undertaking a mutualistic interaction. Indeed, symbiosis with tetrodotoxin-producing *Shewanella* species could explain the impressive toxin concentration in some cephalopods, such as the blue-ringed octopuses of the *Hapalochlaena* genus. Evidences of the presence of *Shewanella* in other molluscs containing high concentrations of tetrodotoxin (Chau *et al.* 2013; Magarlamov, Melnikova and Chernyshev 2017) are consistent with this proposal.

Besides these specific interactions, *Shewanella* species are also known to be part of the intestinal microflora of numerous other metazoans. They have been isolated from the intestinal tract of various organisms such as fishes (Satomi, Oikawa and Yano 2003; Li, Xie and Li 2016; Lloyd, Nazaret and Barkay 2018), arthropods (Chaiyapechara *et al.* 2012; Li *et al.* 2012; El-Sayed and Ibrahim 2015;

Ayayee *et al.* 2017; Huang *et al.* 2019), molluscs (Kim *et al.* 2007; Richards *et al.* 2008) and echinoderms (Hong *et al.* 2017) (Fig. 4). The stable presence of prokaryotes in the intestinal tract is not only due to transitory diet since *Shewanella* strains have been shown to act as probiotics to protect eukaryotes from pathogens (Vidal *et al.* 2016). Metazoans could also be supplied with eicosapentaenoic acid (EPA) and omega-3 fatty acids produced by bacteria (Hau and Gralnick 2007; Dailey *et al.* 2016). As a counterpart, the metazoans offer a nutrient-rich and protective ecological niche to the bacteria.

Similarly, specific *Shewanella* species belong to the epibiotic bacterial communities associated with corals (Cnidarians) and sponges (Porifers) (Lee *et al.* 2006; Yang *et al.* 2006; Shnit-Orland, Sivan and Kushmaro 2010; Dupont *et al.* 2014; Rua *et al.* 2014; Laport *et al.* 2017; Vijayan *et al.* 2017) (Fig. 4). Interestingly, sponge-associated *Shewanella* species cluster together in phylogenetic analyses and present specific genomic features, suggesting a symbiotic specialisation of this branch of the genus (Alex and Antunes, 2019).

In contrast to the apparently favourable influence of *Shewanella* species on numerous aquatic metazoans, members of the genus are involved in infections of the same organisms. Indeed, some strains have been shown to be pathogens of fishes or molluscs under some conditions (Gu and Mitchell 2002; Cai *et al.* 2006; Esteve, Merchán and Alcaide 2017), they have also been detected in arthropod haemolymph, repressed by the eukaryotic immune system (Sun *et al.* 2018). If some strains, like *S. algae*, seem to be specialised in nocive interactions, others exhibit more opportunistic behaviour. In general, an outbreak of *Shewanella* seems to trigger pathogenic behaviour, responsible for metazoan infections (Esteve, Merchán and Alcaide 2017). Thus, for a given organism, *Shewanella* species could be friend or foe, depending on the species encountered, the host state and/or the environmental conditions.

Photosynthetic organisms

Aquatic photosynthetic organisms belong to different kingdoms: bacteria and eukaryotes. Among eukaryotes, these organisms belong to SAR (stramenopiles, alveolates and *Rhizaria*) and *Plantae* superkingdoms (Fig. 4, Burki 2014).

The *Plantae* kingdom includes not only red and green algae, but also flowering plants. *Shewanella* species have been isolated on and near all of these groups, from red algae to the rare marine flowering plants (Fig. 4) (Simidu *et al.* 1990; Borsodi *et al.* 2007; Wang *et al.* 2016; Lujan, Eisen and Coil 2017). However, the reasons for the presence of the bacteria in this environment are not understood. Some species can degrade the polysaccharides that are produced by algae and can act on dead organisms or litter degradation without further interaction (Martin *et al.* 2015; Yagi *et al.* 2018). On the other hand, it was shown that *S. algae* acts on sporulation of the red alga *Gracilaria dura* (Singh *et al.* 2015), suggesting a bacterial role in the life cycle of the photosynthetic organism and, therefore, a more specified relationship. Reciprocally, some eukaryotes also impact the neighbouring microflora. For instance, dimethylsulfoniopropionate (DMSP) is a molecule synthesised by photosynthetic organisms that impacts microorganisms. Although its exact role is not fully understood, it seems that DMSP acts on bacterial colonisation of algae. Moreover, DMSP can also be detected by few bacteria and, thus, could serve as a signalling molecule during alga-bacteria symbiosis (Todd *et al.* 2007; Saha *et al.* 2012). Although it is premature to speak about *Plantae-Shewanella* symbioses, some results point in that direction, and further work must be carried out to establish or discard such a proposal.

Despite their apparent similarity to red and green algae, brown algae belong to a totally different superkingdom of eukaryotes: SAR and more precisely, its stramenopile constituent (Fig. 4) (Burki 2014). The SAR superkingdom also contains diatoms and dinoflagellates. Another phylum, the haptophytes, are closely related to this superkingdom, as well (Fig. 4). *Shewanella* species have been

also found on and around brown algae (Fig. 4) (Martin *et al.* 2015; Kim *et al.* 2016) and their impact is thought to be similar to that described for other algae. Brown algae also have mechanisms to avoid bacterial settling on organisms, suggesting that *Shewanella* species can have deleterious effects on the alga (Plouguerné *et al.* 2010). To our knowledge, *Shewanella* isolates sampled from organisms from *Plantae* and SAR superkingdoms belong to different species, suggesting specificity between bacteria species and algae for the putative symbiosis.

Diatoms, which are important primary producers of the marine medium and that belong to the stramenopiles clade, could also form specific interactions with *Shewanella* species (Fig. 4). Indeed, in Antarctic polar environments, the presence of diatoms seems to be necessary for microbial communities, including *Shewanella* species (McGrath Grossi, Kottmeier and Sullivan 1984; Bowman *et al.* 1997). A *Shewanella*-diatom symbiosis could thus occur, even if the nature of the interaction is not known. The anti-freeze proteins from *Shewanella* species could be important for diatoms, preventing freezing of the surrounding medium (Vance, Graham and Davies 2018).

A recent study indicates that *S. oneidensis* is actively attracted to another photosynthetic eukaryote, *Emiliania huxleyi* (Petit *et al.* 2015). This organism belongs to the Haptophytes, a clade closely related to the SAR superkingdom (Fig. 4). Using senescent phytoplankton, it was shown that the bacterium actively swims toward the dying organisms through chemotaxis, supposedly to sustain its development from phytodetritus. Although the experiments were performed with senescent eukaryotes, the experiment with healthy organisms was not carried out and it is thus possible that the bacteria could also benefit from healthy organisms, indicating a beneficial interaction.

In most cases, *Shewanella* species are believed to be beneficial to photosynthetic organisms by, at least, recycling organic matter. Nevertheless, another mechanism is possible. Indeed, in described *Plantae*-bacteria symbioses, the prokaryotes are involved in providing nitrogen to the eukaryotes by either nitrogen fixation or degradation of amino acids (Suzaki, Yoro and Kawaguchi 2015; Carvalho *et al.* 2016; Calatrava *et al.* 2018). In return, photosynthetic organisms provide carbon sources, such as glycerol, to bacteria through carbon fixation, enabling both organisms to survive despite starvation. Since *Shewanella* species have the ability to use amino acids as nitrogen sources and glycerol as a carbon and energy source, they could possibly supply photosynthetic organisms with nitrogen and assimilate the glycerol produced. More complex symbioses with photosynthetic organisms could then occur, explaining the presence of bacteria with the eukaryotes. Thus, further studies must be carried out to decipher if the presence of *Shewanella* is episodic or specific.

As for metazoans, *Shewanella* species can also harm photosynthetic organisms. Indeed, the strain *Shewanella* sp. Lzh-2 has been shown to act on the declining phase of cyanobacterial blooms through the production of algicidal molecules (Li *et al.* 2014). Bloom decline triggers a nutrient increase, favourable to the *Shewanella* population. They have been also shown to be abundant during declining phase of bloom of dinoflagellates, organisms belonging to the SAR superkingdom (Fig. 4) (Basu *et al.* 2013). However, in the case of dinoflagellates it is yet not proved that the bacteria present any direct deleterious effect on the eukaryote.

Coevolution theory

As described above, the *Shewanella* genus undertakes putative long-term interactions with organisms belonging to various superkingdoms of eukaryotes (Fig. 4). Considering putative, suspected, and proven symbioses, it appears that these bacteria interact with distantly related branches of organisms within superkingdoms. This is particularly evident for organisms in the *Plantae* superkingdom, where at least one case of interactions can be found in each group since the separation with the glaucophytes, or in the metazoan clade of the opisthokonts in which symbioses are suspected in every clade except the little studied ctenophors (Fig. 4). Similarly, the *Shewanella* genus appears to interact with different members

of the SAR superkingdom and with its sister clade, the haptophytes (Fig. 4). Within these phyla is found the majority of multicellular eukaryotes, which are also the most studied (Burki 2014). Moreover, the unicellular clades in which *Shewanella* species interactions are at least suspected, namely diatoms and haptophytes, are among the best investigated unicellular eukaryotic groups. From these results it can be postulated that these bacteria established symbioses with eukaryotic organisms since the separation of early phyla within superkingdoms and, thus, that they coevolved with the developing branches of eukaryotes.

Although purely speculative, this hypothesis is supported by experimental data and isolates, as described above. Thus, in addition to the necessity of investigating of the described putative interactions, it could be interesting to look for potential interactions with *Shewanella* species among “missing” phyla, such as ctenophors, aquatic fungi, glaucophytes, or the numerous unicellular clades of the SAR superkingdom, but also the rest of the eukaryotic phylogenetic tree (Fig. 4). If confirmed, these ancient interactions would have some consequences for current organisms. As an example, symbioses with the mobile metazoans could explain the large geographical and niche expansion of the genus, moving out from the original hydrothermal-mat ecological niche and causing the diversification observed in the current species (Zhong *et al.* 2018).

Prokaryotes

The redox-stratified environments where most *Shewanella* species are found are rich ecological niches containing various organisms. As numerous strains assimilate fermentation end-products, such as formate, lactate, or pyruvate, but cannot use simple or complex sugars, some authors have assumed that survival of some *Shewanella* species may be sustained by fermentative bacteria that share the same biotope (Nealson and Scott 2006; Choi *et al.* 2014). In return, dioxygen consumption by the *Shewanella* species and the production of acetate coupled with assimilation of fermentation end-products allows for the survival of syntrophic partners (Nealson and Scott 2006). A similar interaction has been recreated under laboratory conditions (Wang *et al.* 2015).

Shewanella species are able to grow using elemental sulphur as an electron acceptor (Moser and Nealson 1996; Nealson and Scott 2006). These bacteria are also resistant to H₂S which they produce. Thus, Nealson and Scott (2006) proposed that *Shewanella* species should also share their ecological niches with sulphate-reducing bacteria in the redox stratified environments. The mechanism of syntrophy would be similar to that of fermentative organisms.

Bacteria-bacteria interactions have also been underlined in works dealing with the recycling of organic matter (Jie *et al.* 2018; Zhu *et al.* 2018). Indeed, it has been shown that during degradation of refrigerated shrimps by a complex microbial population the quorum sensing mechanism impacts *Shewanella* growth, even if the strain used in this work is unable to synthesize any autoinducer (Jie *et al.* 2016). Thus, this work indicates that the production of signalling molecules from other microorganisms modifies *Shewanella* genus behaviours. This highlights the existence of interspecies interactions based on specific signal molecules. However, the type of interaction occurring in this case (mutualistic, opportunistic) is unknown. On the contrary, it has been shown that some bacterial strains can inhibit and be inhibited by *Shewanella* biofilm formation during fish spoilage (Zhu *et al.* 2018). Thus, the impact on *Shewanella* growth is organism-dependent, supporting the hypothesis of the existence of specific bacteria-bacteria interactions.

Human-derived ecological niches

Human activities have an impressive impact on biotopes: some are modified due to our presence, but totally new biomes are also created. Thanks to their physiological versatility and their natural

adaptability, *Shewanella* species could survive these modifications and would also colonise these recently created environments.

Many species from the *Shewanella* genus are known not only for their resistance to toxic compounds but also for their ability to detoxify their surroundings. For instance, the strain *S. putrefaciens* 200 has been isolated from a sample of crude oil (Obuekwe, Westlake and Cook 1981). In fact, numerous *Shewanella* strains have been detected in oil- and fuel-contaminated environments and have been shown to degrade these hydrocarbides in some cases (Gentile *et al.* 2003; Martín-Gil, Ramos-Sánchez and Martín-Gil 2004; Deppe *et al.* 2005; Gerdes *et al.* 2005; Gao *et al.* 2015; Suganthi *et al.* 2018). Similarly, *Shewanella* sp. ANA-3 has been isolated from an environment strongly contaminated with arsenic, a toxic element that can be used in its oxidised form by the bacterium as a respiratory substrate (Saltikov *et al.* 2003). Sulphur and metal-rich waters produced by acid mine drainage, a process due to mining activities, constitute a favourable environment for *Shewanella* species, which are able to use these compounds as respiratory substrates (Sravan Kumar *et al.* 2010; Sun *et al.* 2015, 2016). Similarly, the bacteria *S. halifaxensis*, *S. canadensis*, and *S. atlantica* have been isolated from a submerged munition dumping area and can degrade some constituents of explosives (Zhao *et al.* 2006, 2007). Even extremely polluted water can be inhabited by *Shewanella* species, such as detergent-rich carwash effluent tanks and drains (Sibanda, Selvarajan and Tekere 2017).

Combining various adaptation mechanisms, the genus has also colonised some totally synthetic environments. These organisms can be found in petroleum industries, on oil or related products, in cooling systems (Obuekwe, Westlake and Cook 1981; Chen *et al.* 2008) and in wastewaters (Sibanda, Selvarajan and Tekere 2017). Some *Shewanella* species are also present in industrial and domestic wastewater treatment plants, degrading organic matter and synthetic products, despite the elevated concentration of toxic compounds (Xu *et al.* 2005; Chi, Chen and Liu 2009; Wu *et al.* 2009). As psychrotolerant saprophytes, presenting robust growth at low temperature and versatile fermentative and respiratory behaviour, some strains pullulate in cold rooms, sustained from diverse alimentary products (Derby and Hammer 1931; Russell, Fletcher and Cox 1995; Pournis *et al.* 2005; Janda and Abbott 2014).

Shewanella species may be involved in human infections, though infrequently. A review published in 2014 describes and discusses the current knowledge of the putative involvement of *Shewanella* genus in human diseases (Janda and Abbott 2014). Documented illnesses linked to the genus include otitis, diarrhoea, soft-tissue infections, septicaemia and both hepatobiliary and pancreatic pathologies. From the different studies, it appears that only multi-species infections are described and that a few species are concerned, the strain *S. algae* being detected in most clinical isolates. It is still unclear if real pathogenic *Shewanella* species exist, or if the clinical isolates reflect an opportunistic behaviour. The apparent recent increase of clinical cases associated to the genus will hopefully bring more insights about the potential pathogenicity of the genus in the near future.

Biotechnological interest

Due to the physiological and ecological-niche versatility of the genus, but also to specific features like EET (Beblawy *et al.* 2018), *Shewanella* species can be perfectly suitable for different biotechnological applications. A non-exhaustive description of the applications already used is presented below.

Probiotics

As numerous species maintain beneficial interactions with marine organisms, *Shewanella* strains are used as probiotics in fish farming (Vidal *et al.* 2016). The addition of these in alimentation or in the medium protects fishes, molluscs, or echinoderms from infections, without any apparent sanitary issues

or side effects (Nayak 2010; Chi *et al.* 2014; Cordero *et al.* 2016; Vidal *et al.* 2016). Reciprocally, use of the algaecide properties of some strains to counteract cyanobacterial or micro-algal efflorescences, which can have dramatic consequences on aquatic environments, have been proposed (Li *et al.* 2014).

Enzymes and products

Enzymes of biotechnological interest have already been purified from *Shewanella* species, such as the denaturation-resistant alginate lyase from *Shewanella* sp. YH1 (Yagi *et al.* 2018) and the thermotolerant alkali-tolerant lipase from *S. algae* (Joseph and Chakraborty 2017). These enzymes could possibly have applications in food industries and polyunsaturated fatty acid production, respectively. Biomaterial production strategies involving *Shewanella* strains have been developed (Pan and Chen 2019). These bacteria can also be used to synthesise diverse products used in food and pharmaceutical industries, such as polyunsaturated fatty acids (Dailey *et al.* 2016; Moi *et al.* 2018), the butter flavouring compound acetoin (Bursac, Gralnick and Gescher 2017), or even antitumoral alkaloids called shewanellines (Wang *et al.* 2014). The genetic and physiological diversity of the genus suggests that numerous other interesting enzymes or products could still be discovered.

Bioremediation

Most of the biotechnological applications implicating *Shewanella* species concern bioremediation. *Shewanella* strains can be used for degradation of hydrocarbides (Gentile *et al.* 2003; Martín-Gil, Ramos-Sánchez and Martín-Gil 2004; Deppe *et al.* 2005; Gerdes *et al.* 2005; Hassanshahian 2014; Suganthi *et al.* 2018), dyes (Xu *et al.* 2005; Chen *et al.* 2008; Hong and Gu 2010; Cai *et al.* 2012; Patel and Bhatt 2015; Ito *et al.* 2016; Liu *et al.* 2018, Lemaire *et al.* 2019), antibiotics (Mao *et al.* 2018; Wang *et al.* 2019), pesticides (Chen and Rosen 2016), synthetic pollutants (Petrovskis, Vogel and Adriaens 1994, de Santana *et al.* 2019) and toxic oxides, such as chromate or tellurite (Baaziz *et al.* 2017; Soda *et al.* 2017; Valdivia-González *et al.* 2017; Wang *et al.* 2017; Meng *et al.* 2018, Lemaire *et al.* 2019). The ability of the *Shewanella* genus to reduce metals extracellularly is also important for bioremediation (Beblawy *et al.* 2018; Zou *et al.* 2018). Indeed, the reduced form of the metal is often less soluble and, therefore, less bioavailable than its oxidised counterpart. Thus, bacterial metal reduction is a way to decrease the effective metal concentration in the medium, trapping the toxics in sediment or in biofilms. *Shewanella* species have been shown to reduce, directly or through soluble electronic relays, a wide range of metals, including iron, manganese, mercury, platinum, technetium, vanadium, palladium, and radionuclides like uranium and plutonium (Fredrickson *et al.* 2008; Jiang *et al.* 2012; Maes *et al.* 2017; Wang *et al.* 2017; Lee, Kim and Kim 2018; Zou *et al.* 2018).

By alternating between anaerobic and aerobic growth conditions in the presence of iron, the ability of the facultative aerobic *Shewanella* strains to externally reduce metal leads to the biotical generation of the highly reactive hydroxyl radical HO[•]. This reacts with the surrounding molecules, leading to degradation of the resistant compounds in the culture medium. Different molecules have been shown to be degraded by this process, such as dichlorodiphenyltrichloroethane (DDT), dioxane, cellulose, trichloroethylene, tetrachloroethylene, anthracene, and pyrene (Li *et al.* 2010; Sekar and DiChristina 2014; Sekar, Shin and DiChristina 2016; Sekar, Taillefert and DiChristina 2016; Sekar and DiChristina 2017). Moreover, biological reduction of other metals, like palladium, allows for the formation of nanoparticles that catalyse the degradation of organochloride derivatives, such as PCB (De Windt, Aelterman and Verstraete 2005).

Microbial fuel cell

Biological metal reduction allows for the reduction of electrodes, resulting in the production of electricity. *Shewanella* cells are already used in this process. EET enables the use of diverse products to sustain energy production (Min, Cheng and Logan 2005; Uría *et al.* 2011; Zou *et al.* 2018). The involvement of these bacteria in pure culture or consortium, mimicking their ecological niches, allows for energy production with an even wider range of compounds (Wang *et al.* 2015), and from wastewater sludge (Zhang *et al.* 2017). Furthermore, advanced microbial fuel cell techniques using *Shewanella* species have recently been developed, leading to a wide range of new applications, such as bioremediation, the biofuel production, development of biosensors, and CO₂ fixation (Zou *et al.* 2018).

Conclusions

The global distribution, ecology and biotechnological interest of the *Shewanella* genus is still largely unknown. Two-thirds of the publications on the genus have been published during the last decade. These bacteria have been historically considered as lonely cold-water organisms, but the last decade brought about knowledge nuancing this postulate. The genus exhibits impressive potential for diverse biotechnological applications, from wastewater treatment to anti-tumour molecule production. Biotechnological applications of these organisms are currently being developed based on the increasing knowledge of their bioremediation mechanisms. Moreover, genetic tools and transformation strategies are available and developed for some species to increase their biotechnological capacities and interests (Corts *et al.* 2019). One can predict that these bacteria will become more and more useful for bio-applications in the near future.

Many *Shewanella* strains have become resistant to toxic pollutants, and it is routine to make toxin-resistant strains in the laboratory. This feature is probably exacerbated by the massive anthropogenic inputs of toxic substances in aquatic environments, giving these bacteria a selective advantage. This would explain the apparent profusion of *Shewanella* species in harbours, waste waters, and other polluted environments. Nevertheless, this abnormal burst of bacteria could also drive a modification of the global microbial population, destabilising the whole ecosystems by unbalancing the cycle of matter or deleterious effects on the surrounding organisms, despite the bioremediation activity of the genus. Similar perturbations of microbial population have already been showed to be induced by eutrophication and pollution with herbicide (Arabet *et al.* 2014). The abnormal increase of *Shewanella* population could probably be used as a biomarker to detect alteration of aquatic ecosystems, but also to estimate the resilience capacity of these environments due to bioremediation.

Although an impressive amount of long-term biological interactions between *Shewanella* species and other organisms are suspected, only a few have been investigated. The biological determinants and specificities of these interactions still need to be determined, as well as the exact impact of each organism on the others. Moreover, it is plausible that the genus maintains interactions with a wider range of organisms than what is currently known. Indeed, isolates and experiments underline the interactions of *Shewanella* species with most multicellular clades of eukaryotes, which are by far the most studied. Thus, it is reasonable to hypothesise that symbiosis could also occur within the other multicellular phyla or in the vast but little studied protist lineages. If confirmed, this large and ancient symbiosis “network” must have driven severe modification of the *Shewanella* genus, such as its distribution, physiology and ecology, but also eukaryotes evolution.

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Conflict of interest

None declared.

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Figures

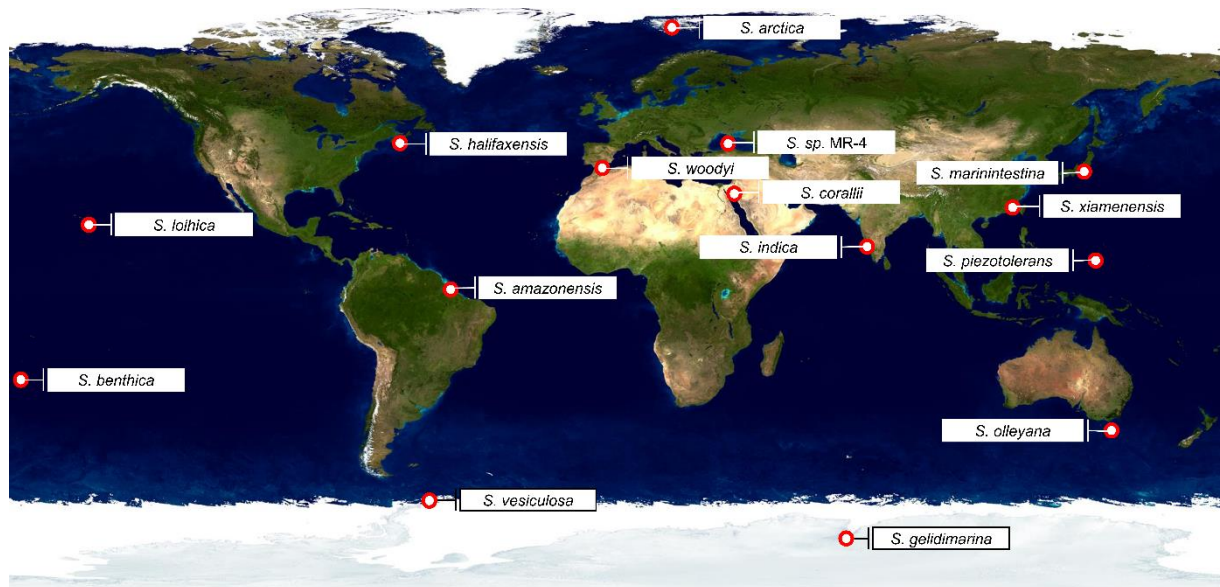


Figure 1. Geographic origin of 15 *Shewanella* species. Respective first-isolation sites are shown on the Visible Earth “Blue Marble” image (NASA Goddard Space Flight Center). The species were arbitrarily chosen to illustrate the geographical distribution of the genus (Nealson, Myers and Wimpee 1991; Bowman et al. 1997; Makemson et al. 1997; Venkateswaran et al. 1998; Skerratt, Bowman and Nichols 2002; Satomi, Oikawa and Yano 2003; Gao et al. 2006; Zhao et al. 2006; Xiao et al. 2007; Bozal et al. 2009; Huang, Sun and Zhang 2010; Shnit-Orland, Sivan and Kushmaro 2010; Verma et al. 2011; Kim et al. 2012; Lauro et al. 2013).

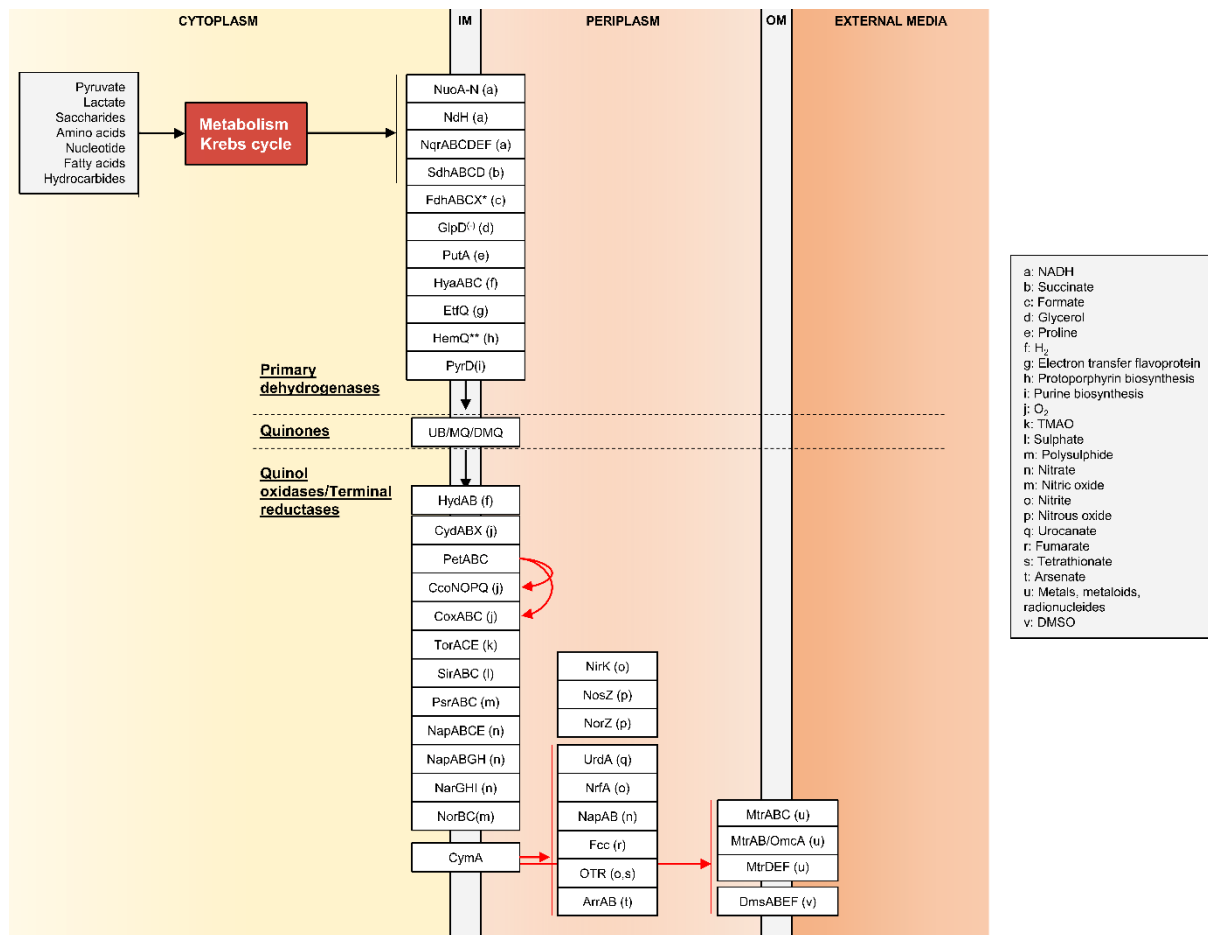


Figure 2. Schematic representation of the respiratory complex described for *Shewanella* species. Direct and indirect (through metabolism and the Krebs cycle) substrates of the respiratory chains are listed in the light grey frame. The symbols * and ** indicate the complexes that are duplicated and triplicated in *S. oneidensis* MR-1, respectively. The symbol (-) indicates that albeit genomic data spotted a putative quinone reducing glycerol dehydrogenase, growth of *S. oneidensis* MR-1 has never been shown. Production of respiratory substrates by metabolism is represented by the horizontal black arrows. Electron transfer to/from the quinone pool is represented by the vertical black arrows. Electron transfers between respiratory complexes are represented by red arrows. IM, inner membrane; OM, outer membrane; ETF, electron transfer flavoprotein; OTR, octahem tetrathionate reductase; UB, ubiquinone; MQ, menaquinone; DMQ, demethylmenaquinone.

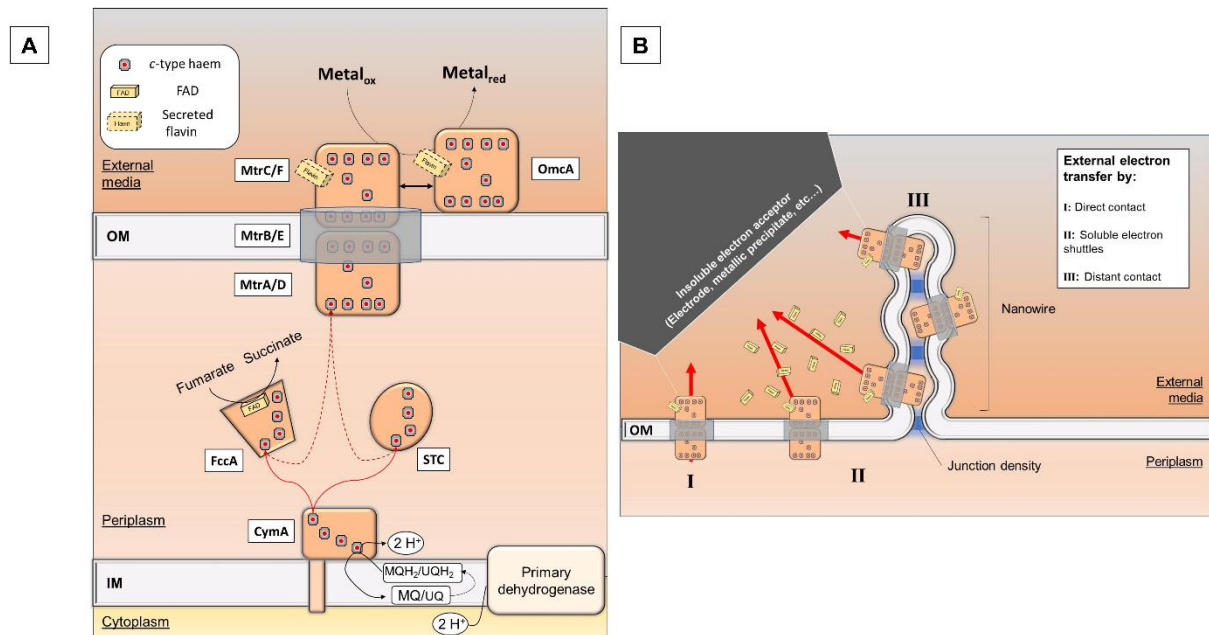


Figure 3. Schematic representation of the external electron transfer mechanism in *Shewanella* species. **A**) Electron transfer from the inner membrane to the external face of the outer membrane. Direct CymA-mediated electron transfer is represented by red arrows (Beblawy et al. 2018). Reduced MtrA or its counterpart MtrD can then directly interact with the Mtr system to transfer electrons to the external, outer membrane MtrC, MtrF, and OmcA cytochromes (black arrow). FccA and STC are able to transfer electrons to the Mtr system, as indicated by red dashed arrows (Taylor et al. 1999; Fonseca et al. 2009; Beblawy et al. 2018). Metal reduction occurs on the external face of the outer membrane by the MtrC, MtrF, or OmcA subunits. The existence of the MtrAB/OmcA complex is still debated, albeit OmcA can functionally replace the MtrC cytochrome (Beblawy et al. 2018; Lockwood et al. 2018). The OmcA cytochrome is thus represented as interacting with MtrC, the sole *in vitro* detected interaction (Beblawy et al. 2018). The secreted flavins, indicated by dashed yellow blocks, are represented as enhancing cofactors of the decahaemic cytochromes, coordinated by redox active disulphide depending on the oxygen concentration (Edwards et al. 2015). Schematic representations of the proteins were constructed using the available structural data, even if only monomeric forms are represented (Taylor et al. 1999; Rodrigues et al. 2006; Paixão et al. 2008; Edwards et al. 2014, 2015). MQH₂/UQH₂, menaquinol/ubiquinol; MQ/UQ, ubiquinone/ menaquinone; FAD, flavin adenine dinucleotide. **B**) External electron transfer strategies occurring in *Shewanella* species. Electron transfers can be directly from the Mtr complex to the electron acceptor in the case of direct contact or by excrescence of outer membranes called nanowires (Beblawy et al. 2018; Subramanian et al. 2018). The “junction density” refers to those observed by Subramanian *et al.* (2018). Otherwise, an important concentration of secreted flavins can lead to distant electron transfers, using them as electron shuttles.

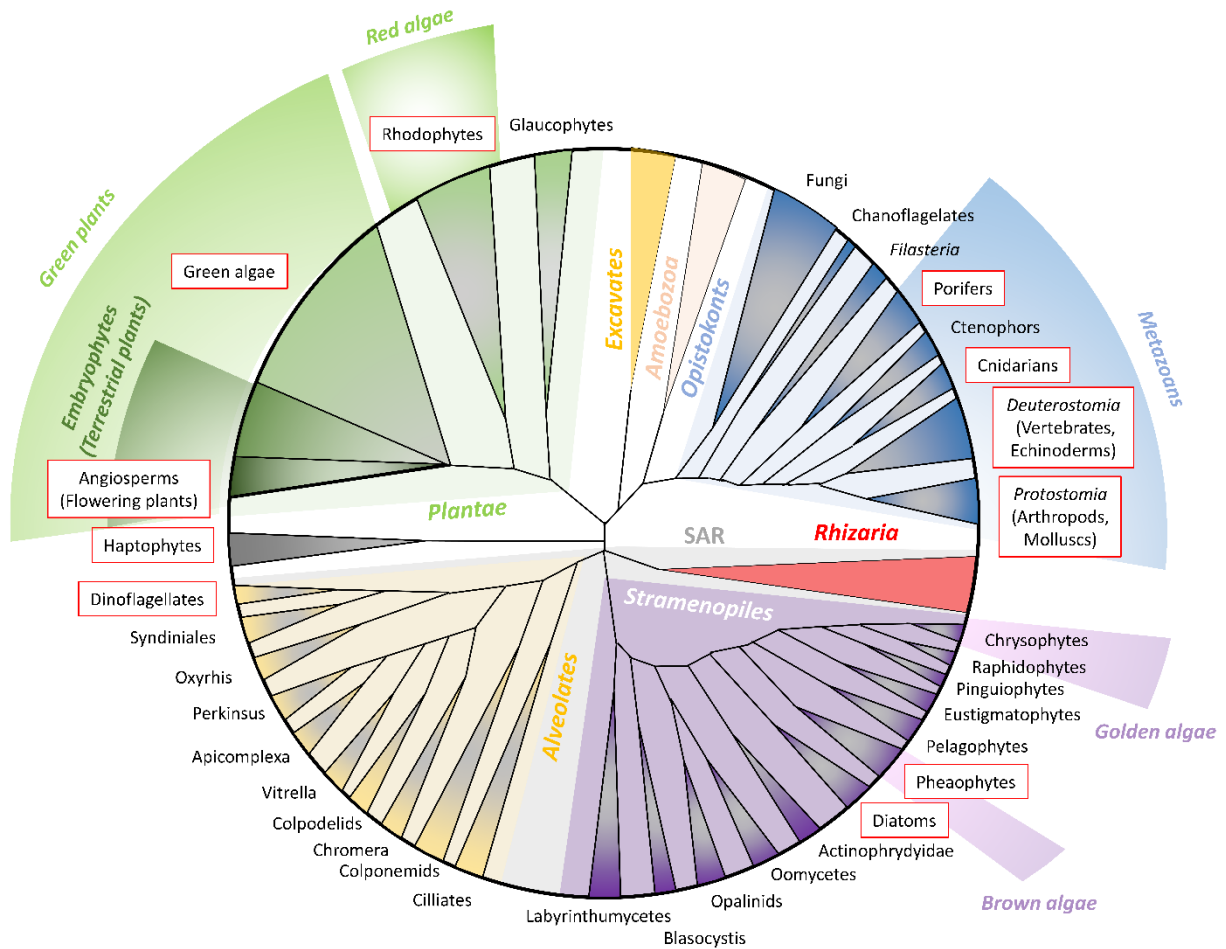


Figure 4. Eukaryotic phyla in which symbioses with *Shewanella* species are suspected or confirmed. Corresponding phyla are framed in red on a schematic representation of the eukaryotic phylogenetic tree constructed based on Burki (2014), with help of the Tree of Life Project (Maddison, Schulz and Maddison 2007). The size of branch and phyla were arbitrarily chosen, and minor branches were excluded to optimise graphical representation. Superkingdoms are highlighted with different colours, as well as the stramenopiles, alveolates and *Rhizaria* constituents of the SAR superkingdom. Vernacular names or inferior clades of interest are indicated around the circular tree.