



REVIEW ARTICLE

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# From cells to power cells: harnessing bacterial electron transport for microbial fuel cells (MFCs)

Sri Sathya Sandilya Garimella<sup>1</sup>, Sai Vennela Rachakonda<sup>1</sup>, Sai Sowmya Pratapa<sup>1</sup>, Gnana Divya Mannem<sup>1</sup> and Ganesh Mahidhara<sup>1\*</sup>

## Abstract

Microbial fuel cells (MFCs), which use bacterial electron transport mechanisms to generate energy, have become a viable technology for renewable energy production. This review investigates the evolutionary and functional connections between bacterial energy transduction mechanisms and mitochondrial electron transport chains, building on the endosymbiont theory of eukaryotic cell evolution. The conserved features and similarities between prokaryotic and eukaryotic electron transport pathways were elucidated, highlighting their common origins and roles in cellular bioenergetics. This discussion explores the essential mechanisms governing the movement of electrons and ions across biological membranes, crucial for generating energy and maintaining electrochemical gradients in bacteria and mitochondria. Capitalizing on these insights, we explore the applications of electrogenic bacteria in MFCs for renewable electricity generation. Optimal conditions for enhancing bacterial electron transfer to electrode surfaces are identified, paving the way for improved MFC performance. Potential large-scale implementations of MFCs in wastewater treatment, biosensing, and bioremediation of contaminated environments are discussed, underscoring their versatility and environmental benefits. The importance of investigating bioenergetic mechanisms at both the cellular and molecular scales of fully harnessing the capabilities of microbial energy conversion systems is highlighted in this review. By bridging the gap between fundamental cellular processes and sustainable technologies, we aim to advance renewable energy solutions that harness the remarkable capabilities of electrogenic microorganisms.

**Keywords** Endosymbiont theory, Intermembrane space, Electrochemical gradient, NADH dehydrogenase, Mitochondrial membrane potential, Electrogenic bacteria, Mitochondrial autophagy, ROS, Microbial fuel cells

<sup>†</sup>Sri Sathya Sandilya Garimella, Sai Vennela Rachakonda, Sai Sowmya Pratapa, Gnana Divya Mannem and Ganesh Mahidhara contributed equally to this work.

\*Correspondence:

Ganesh Mahidhara  
gmahidha@gitam.edu

<sup>1</sup>Department of Biotechnology, GIS, GITAM University,  
Visakhapatnam 530 045, India



## Introduction

### Eukaryotic and bacterial relationship

Endosymbiosis hypothesis gives an informative explanation of the genesis of eukaryotic cells by symbiotic integration of prokaryotic cells. This hypothesis was first proposed by famous botanist Konstantin Mereschkowski and then supported by Lynn Margulis via empirical data (Gray 2017). According to this notion, larger cells absorbed tiny bacteria that were not digested but instead managed to thrive within their host, resulting in a symbiotic connection. The evolutionary origin of heterotrophic eukaryotic cells is broadly understood (Martin et al. 2015). Furthermore, the integration of photosynthetic bacteria by bigger cells resulted in the creation of autotrophic eukaryotes (Blankenship 2010; Martin et al. 2015). This engulfment dynamic, in which a eukaryotic cell consumes an aerobic prokaryote, culminates in an endosymbiont interaction with the host, paving the path for mitochondrial development (Zimorski et al. 2014). When these mitochondria-rich cells engulfed photosynthetic prokaryotes they evolved into chloroplasts, which are specialized cell organelles (McFadden and Van Dooren 2004). Surprisingly, the size of these mitochondria and chloroplasts is comparable to that of bacteria. Furthermore, when separated, they display the ability to split independently (Wallin 1927; Martin et al. 2015). Moreover, these cellular structures serve as pivotal players in transforming solar energy into a practical form within the biosphere. Within these endosymbionts, electron transport produces proton gradients, culminating in the creation of ATP as free energy.

Though in distinct contexts and via different processes, mitochondrial electron transport, bacterial electron transport, and mitophagy all have significant roles in energy generation and cellular health (Gustafsson and Dorn 2019). By producing ATP through oxidative phosphorylation, mitochondria generate cellular energy and are hence referred to as cellular powerhouses (Brand et al. 2013). Mitophagy, on the other hand, is a biological mechanism that eliminates malfunctioning or damaged mitochondria. However, if a mitochondrion malfunctions, the electron transfer cycle is disrupted, resulting in a drop in ATP synthesis and, as a result, cellular stress.

An essential step in the bacterial process of energy generation is the distribution of ions throughout the cellular membranes during electron transfer. An electrical gradient is created when electrons transfer, resulting in an influx of ions that can power other cellular processes or generate ATP (Tahernia et al. 2020). These energy generation and maintenance mechanisms entail electron and ion transport, which contributes to cellular energy balance and overall cell function (Ahmad et al. 2023).

Mitochondrial and bacterial electron transport chains share a common evolutionary origin and function by

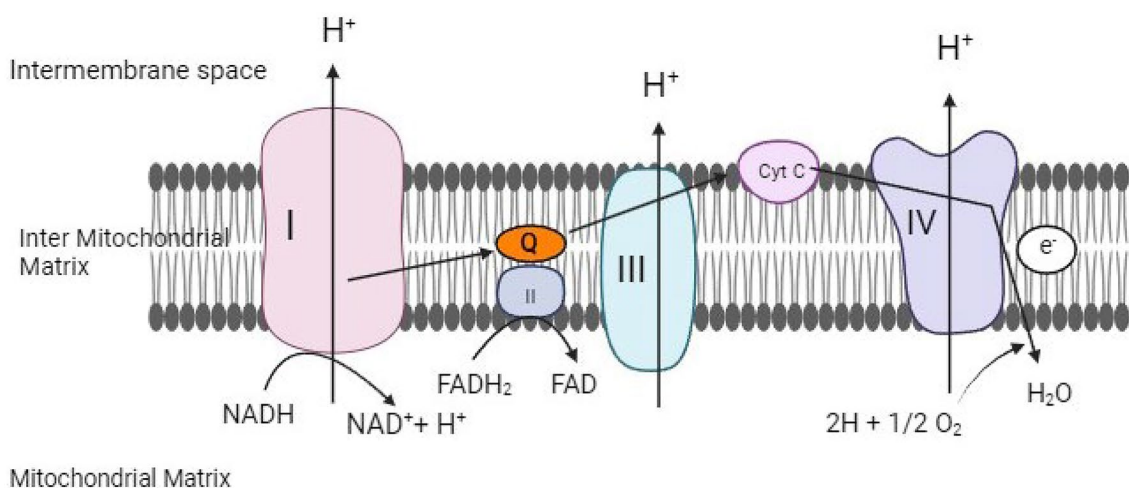
similar principles of electron flow to generate membrane potentials and harness energy, however they have adapted distinct structures and mechanisms that suit the specific energy demands within their respective eukaryotic and prokaryotic cellular environments; the delicate regulation of these electron transport processes impacts core physiological functions in cells from energy production to signaling pathways, and their emerging applications in areas ranging from bioremediation to bioenergy generation and biomedical therapies highlight the significance of further exploring bioenergetics at the cellular and subcellular levels.

### Mitochondrial electron transport

The electron transport chain (ETC), essential for aerobic energy synthesis, is mostly found in the inner mitochondrial membrane, which contains many enzymes (Van Hellemond and Tielens 1994). The bacterial origin hypothesis in mitochondria proposes that mitochondria gained their structural and functional properties from bacteria through the process of endosymbiosis. Mitochondria have a bilayer membrane structure with an inner and outer membrane. The intermembrane gap between these two membranes contains a matrix that houses the ETC structure [Fig. 1].

Important metabolic processes including the Krebs cycle and  $\alpha$ -oxidation take place inside the mitochondrial matrix, generating NADH and  $FADH_2$ . These molecules transport electron reducing equivalents, which are subsequently channelled to a sequence of enzyme complexes (Tielens 1994; Van Hellemond and Tielens 1994). The inner mitochondrial membrane is home to four of these enzyme complexes, which are indicated by the Roman numbers I-IV. In the process of releasing energy, the reducing equivalent electrons go throughout these complexes, from the first to the fourth (Cecchini et al. 2002). Transporting hydrogen ions from the mitochondrial matrix to the intramembranous region requires the energy generated. This continual ion movement causes a larger concentration of hydrogen ions in the intermembranous region than in the mitochondrial matrix, resulting in an electrochemical gradient (Hederstedt and Ohnishi 1992). Hydrogen ions cannot pass over the electrochemical gradient because the inner mitochondrial membrane is impermeable (Friedrich et al. 1995).

At this point, the enzyme ATP synthase steps in to act as a unique transporter. This enzyme promotes the return of hydrogen ions to the mitochondrial matrix, capturing the energy created by this ion transport (Fenchel et al. 2012). Thus, the enzyme facilitates the conversion of adenosine diphosphate (ADP) to adenosine triphosphate (ATP), which leads to the production of energy in the form of ATP. The four enzyme complexes'

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**Fig. 1** As the process uses energy, the NAD<sup>+</sup> and H<sup>+</sup> that NADH dehydrogenase dehydrogenated from NADH are transported from the mitochondrial matrix to the inter-mitochondrial matrix. Protons (H<sup>+</sup>) are therefore released into intermembrane space by complex 1. After removing the hydrogen from the succinate and oxidizing it to fumarate (FADH to FADH<sub>2</sub>), which is engaged in the Krebs cycle, complex two uses the residual energy from complex one. The movement of electrons from complex II to complex III is aided by cytochrome Q. Accepting and sharing electrons from the electron transport chain with complex IV is complex III's important function. After obtaining the electrons, the complex uses them to convert oxygen to water. The electron transport chain in mitochondria is seen above, while the bacterial electron chain consists of just three complexes: terminal oxidase, quinone pool, and succinate dehydrogenase

sequential movement is the key to this energy generation system (Table 1).

- 1) NADH dehydrogenase is Complex I of the electron transport chain. The two arms of the L-shaped protein complex are the horizontal arm located in the mitochondrial matrix and the vertical arm located in the inner mitochondrial membrane (Hederstedt and Ohnishi 1992). The dehydrogenase in this complex takes hydrogen from the reduced form of their nicotinamide at any dinucleotide, and it is referred to as a complex since it also contains flavin mononucleotides (Van Hellemond and Tielens 1994; Lengeler et al. 2009).
- 2) The succinate dehydrogenase complex is complex II of the ETC (Hederstedt and Ohnishi 1992). This enzyme is known as a dehydrogenase because it is capable of removing hydrogen from compounds. In this instance, it will do so by oxidizing succinate to fumarate, a step in the Krebs cycle. Because it includes iron-sulfur complexes in addition to succinate dehydrogenase II complexes, which are
- a component of the Krebs cycle and catalyze the reaction that oxidizes succinate to fumarate, it is known as a complex (Hederstedt and Ohnishi 1992; Nelson et al. 2008).
- 3) The enzyme cytochrome reductase is located in Complex III of the ETC. Q, cytochrome C oxidase reductase is another name for it (Van Hellemond and Tielens 1994; Nicholls 2003). Proteins known as cytochromes have heme as part of their complexes or prosthetic groups. They also include an iron core, where the presence of electrons determines whether the iron is reduced or oxidized: Cytochrome B, Cytochrome C1, and Cytochrome C are the three kinds of cytochromes found in it. Electrons from the electron transport chain are mostly taken up by Complex III and sent to Cytochrome C, which then sends the electrons to Complex IV of the electron transport chain (Nicholls 2003).
- 4) Complex IV is the enzyme known as cytochrome C oxidase. Cytochrome C is oxidized by a complex that contains copper and heme. It is called cytochrome C oxidase because it uses the electrons from

**Table 1** The main complexes in cellular respiration's electron transport chain (ETC). It gives details on each complex, which are referred to as Complex I through Complex IV, including its name and purpose. The electron transport chain, ETC, is made up of many protein complexes that are found in the inner membrane of the mitochondria. They help move electrons from electron suppliers like NADH to electron acceptors like oxygen. Protons are pumped across the membrane in conjunction with this process to create an electrochemical gradient that powers ATP production

Complex	Name	Function
I	NADH dehydrogenase	protein complex in the shape of a I, with one vertical arm located in the inner mitochondrial membrane and one horizontal arm located in the mitochondrial matrix. It includes flavin mononucleotides and extracts hydrogen from NADH.
II	Succinate dehydrogenase	Removes hydrogen from succinate, oxidising it to fumarate in the Krebs cycle. Contains iron-sulfur clusters.
III	Cytochrome reductase(Q-cytochrome c oxidoreductase)	Transfers electrons from the electron transport chain to cytochrome c. Contains cytochrome b, c1 and c, which have heme and iron cores
IV	Cytochrome c oxidase	Oxidize cytochrome c, using electrons to reduce oxygen to water. Contains copper and heme. They are involved in proton pumping and ATP synthesis.

cytochrome C to reduce oxygen to water (Van Hellemond and Tielens 1994; Stumm and Morgan 2012). The production of  $\Delta\mu\text{H}^+$  at proton pumps causes a reversal of the ATP synthase complex and a block of electron transport in the mitochondrial chain, both of which are caused by cytochrome oxidase (Stumm and Morgan 2012).

When ions pass through the complexes and across the membrane, a potential for the membrane known as the mitochondrial membrane potential is generated (Thauer et al. 1977). This potential is essential for sustaining an electric field, which is represented mainly by a negative charge inside the inner part of the mitochondria. This potential is influenced by the positively charged elements of the cell, such as the metal ions, anions, and hydrogen cations. Notably, this mechanism also involves nucleotides that are essential to the electron transport chain, including AMP, GTP, ADP, and ATP (Thauer et al. 1977; Van Hellemond and Tielens 1994).

This electric field facilitates the transport of cations while restricting the passage of anions (Yang and Qin 2021). It utilizes the charge carried by these cations or nucleotides to establish the membrane potential (Van Hellemond and Tielens 1994; Yang and Qin 2021). The mitochondrial membrane potential plays several vital

roles and makes a substantial contribution to the mitochondrial process. It is not just a consequence of the electron transport chain (Thauer et al. 1977).

Anion transit is restricted while cation transport is facilitated by this electric field. The membrane potential is determined by using the charge that these cations or nucleotides carry (Van Hellemond and Tielens 1994). The electron transport chain produces the mitochondrial membrane potential, which is necessary for the synthesis of ATP and the production of cellular energy (Xian and Liou 2021). Furthermore, this potential is essential for preserving mitochondrial function, limiting the generation of reactive oxygen species inside the mitochondria, and regulating cellular metabolism (Kobayashi et al. 2023). The efficiency of energy generation in cells is greatly enhanced by the mitochondrial membrane potential, which plays a vital role in oxidative phosphorylation (Schenkel and Bakovic 2014). Coenzyme Q and cytochrome C are two more prosthetic groups that are integrated via the configuration of electron carrier complexes throughout the inner mitochondrial membrane (Nicholls 2003). The electron transport chain's usefulness and intricacy are further improved by these elements.

#### Bacterial electron transport

Different from mitochondria, bacteria use light to create a proton gradient and ATP as a means of obtaining energy through glycolysis and cell membranes (Friedrich et al. 1995). Because prokaryotes, like bacteria, lack mitochondria, their electron transport chains operate inside the plasma membrane. The transport chains in bacteria bear striking resemblances to those in mitochondria (Tahernia et al. 2020).

NADH is an important electron donor in eukaryotes. In the related electron transport chain, complexes I, III, and IV function as proton pumps, and cytochrome c and Q function as mobile electron carriers. The electron acceptor in this chain, which also includes  $\text{O}_2$ , cytochrome c, complex IV, complex I, Q, and complex III, is molecular oxygen (Nelson et al. 2008). Prokaryotes, which include bacteria and archaea, display a wide variety of electron donors and acceptors in their surroundings. Bacteria can utilize various electron donors such as NADH, succinate, hydrogen, carbon monoxide, ammonia, and sulfur, with oxygen being a common electron acceptor (Rojas et al. 2021). In contrast, archaea also have a complex set of electron acceptors and donors but may differ from bacteria in specific mechanisms due to their unique metabolic pathways and adaptations (Yang and Qin 2021). It is crucial to remember that there are three possible entry points for electrons into a chain: the dehydrogenase level, the quinone pool level, and the mobile phase level.

Bacterial cells typically employ multiple electron transport chains, often simultaneously. Bacteria are capable of

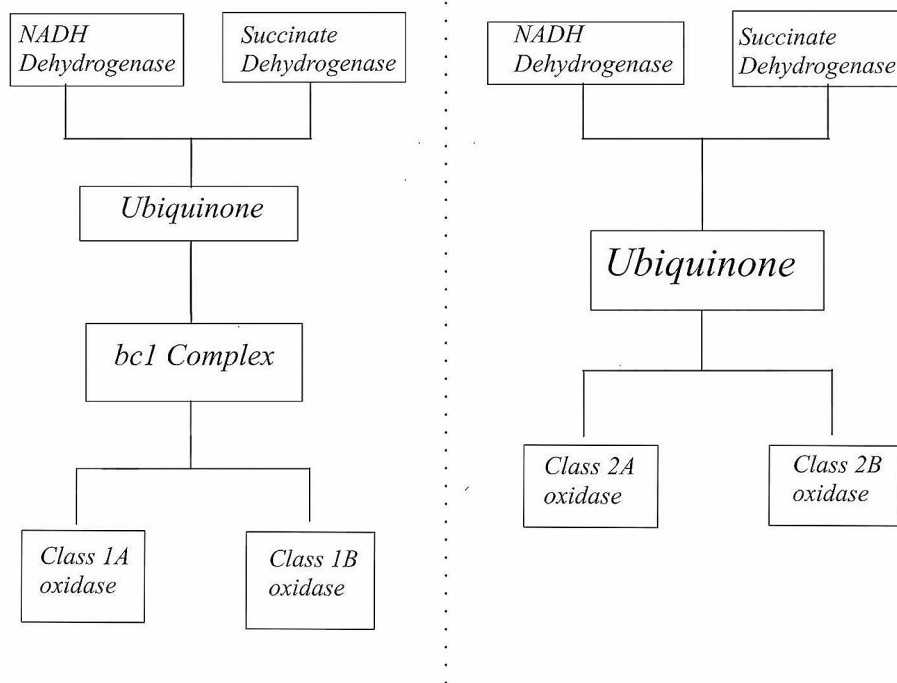
utilizing a plethora of electron donors, oxidases, reductases, and electron acceptors, which include numerous dehydrogenases, oxidases, and reductases (Stumm and Morgan 2012). For instance, *Escherichia coli* (*E. coli*) can utilize two distinct NADH dehydrogenases and two different quinol oxidases, resulting in four separate electron transport chains operating simultaneously during aerobic growth and glucose metabolism (Thauer et al. 1977). A transmembrane proton gradient produces a component that acts as a proton pump in every electron transport chain. Like mitochondria, bacterial electron transport chains can include one to three proton pumps (Voet and Voet 2010).

Because bacteria live in a variety of conditions and have different types of aerobic metabolism, their aerobic respiratory systems have a greater diversity of electron transfer routes than mitochondrial respiratory systems. Quinol oxidases and cytochrome c oxidases are the two types of specialized terminal oxidases that they use (Anraku 1988; Witt et al. 1995). Ferrocyclochrome C is used by class I oxidases to supply electrons, which convert molecular oxygen into water. Heme a and  $\text{Cu}^{2+}$  are present in class IA enzymes, while heme b or heme o are present in class IB enzymes. Bacterial quinol oxidases uniquely transport electrons from ubiquinol and menaquinones to atomic oxygen. While heme G is absent from these enzymes, heme b, heme o,  $\text{Cu}^{2+}$  in Class IIA

or heme b and d in Class IB are present (Anraku and Gennis 1987). The terminal oxidases from Classes IA, IB, IIA and IIB, where class IA is the mitochondrial complex IV's homology, the diversity of oxidases found in bacteria to adapt to varying oxygen levels and aerobic conditions (Pernil and Schleiff 2019). While these oxidases are primarily observed in bacteria, it is of significant interest to explore how archaea, especially those thriving in extreme environments with limited oxygen, may differ in their terminal oxidase systems to suit their unique metabolic requirements and environmental challenges (Borisov and Forte 2021). The adaptation of bacterial terminal oxidases to aerobic lifestyles suggests a complex interplay between different oxidase classes to efficiently utilize oxygen as an electron acceptor, a feature that may vary in archaeal systems based on their distinct evolutionary pathways and environmental niches (Nealson and Popa 2005). Further research into the terminal oxidase systems of archaea could provide valuable insights into the evolutionary divergence and functional adaptations of these organisms compared to bacteria in response to diverse environmental conditions (Fig. 2).

#### Similarities between bacterial and mitochondrial electron transport chains

The capacity of bacteria to use a variety of electron sources is impressive. When organic matter provides the



**Fig. 2** Examples of terminal oxidases from Classes IA, IB, IIA, and II B. Class I and II oxidases are cytochrome c oxidases and ubiquinol oxidases, respectively. The other three oxidases are only found in bacteria, but Class IA oxidase is the mitochondrial complex IV's homolog. Bacteria typically have several terminal oxidases to adapt to the aerobic mode of life and changes in oxygen tension

energy, succinate, NADH or succinate dehydrogenase enters the electron transport chain and acts similarly to Complex II in mitochondria (Unden and Bongaerts 1997). Glyceraldehyde-3-phosphate dehydrogenase, lactate dehydrogenase, formate dehydrogenase, and H<sub>2</sub> dehydrogenase (hydrogenase) are some other dehydrogenases that process different energy sources. Some dehydrogenases route electrons into the quinone pool, whereas other types act as pumps of protons. The fact that the majority of dehydrogenases are only produced when required suggests that bacteria choose which enzymes from their DNA library to generate depending on the circumstances of their surroundings (Wissenbach et al. 1992; Van Hellemond and Tielens 1994).

Quinones are lipid-soluble, mobile carriers that carry protons and electrons between mobile macromolecules embedded in the membrane more readily than between stationary macromolecules (Gest 1987). Bacteria employ similar quinones such as menaquinone and ubiquinone, which is the same quinone that mitochondria use. A proton pump is a component of all electron transport chains (Gao et al. 2012). It has the ability to physically transmit protons across membranes, as mitochondrial Complexes I and IV demonstrate, or it may move electrons in the reverse way to accomplish the same goal (Wojtczak et al. 1986; Bernardi 1999). The mitochondria's complex III uses the latter type of proton pump, which is mediated by a quinone (the Q cycle) (Zorova et al. 2018).

The Gram-negative, facultatively anaerobic soil bacteria *Paracoccus denitrificans* is used as a model organism in respiration studies. When this bacteria develops aerobically, its electron transport chain consists of four

complexes that resemble the mitochondrial chain (Van Hellemond and Tielens 1994). However, if the bacteria adjusts to anaerobic respiration and starts utilising nitrate as an electron acceptor, the chain reorganizes. Bacterial electron transport chains are usually quite complex and frequently branched since most bacteria are anaerobic and use a variety of electron acceptor components (Kracke et al. 2015). The fact that these chains are often shorter and have lower P/O ratios (As electrons move through the respiratory electron transport chain, the number of ATP molecules produced per oxygen atom consumed is known as the P/O ratio, which is used to gauge how well oxidative phosphorylation coupling is working.) than mitochondrial transport chains suggests that, although sharing similar essential functions, the developmental details of bacterial (prokaryotic) and mitochondrial (eukaryotic) electron transport chains are different.

For example, *E. coli* has an electron transport chain that is structurally different from the mitochondrial chain but forms similar functions, such as moving protons (H<sup>+</sup>) across the plasma membrane and electrons from NADH (the electron donor) to acceptors (Van Hellemond and Tielens 1994). Shorter and with two branches (cytochrome d and cytochrome o), the *E. Coli* chain contains a wide variety of cytochromes. Both branches grow differently, and Coenzyme Q (ubiquinone) is a transporter that supplies electrons to each (Gest 1987). The cytochrome o branch performs well at high oxygen levels whereas the cytochrome d branch operates at low oxygen levels and is less efficient (Gest 1987; Van Hellemond and Tielens 1994) (Table 2).

**Table 2** Similarities between bacterial and mitochondrial electron transport chains: while both bacterial and mitochondrial ETCs share some common components like quinones and proton pumps, they differ in aspects like structure, efficiency, terminal electron acceptors and oxygen tolerance. Bacterial ETCs are more versatile while the mitochondrial ETC is more standardised and optimized for aerobic respiration

Feature	Mitochondrial Electron Transport Chain	Bacterial Electron Transport Chain
Electron donors	NADH, FADH <sub>2</sub>	NADH, succinate, various hydrogenase enzymes
Mobile carriers	Ubiquinone	Quinones like menaquinone, ubiquinone
Proton pumps	Present in complexes I, III, IV	Present in some complexes
Terminal electron acceptors	Molecular oxygen (O <sub>2</sub> )	O <sub>2</sub> , nitrate, sulphate, CO <sub>2</sub>
Structure	Linear, standardized set of complexes	Often branched, more variety in cytochromes
Efficiency	Longer, higher P/O ratios	Usually shorter, lower P/O ratios
Oxygen tolerance	Optimised for aerobic respiration	Many variants for low or high-oxygen

### Electrogenic bacteria that power microbial fuel cells

Due to their electron transport system, electrogenic bacteria have the unusual capacity to produce electricity (Palikaras et al. 2015). In low-oxygen settings, these microbes eliminate surplus electrons by moving them to extracellular acceptors, which generates a current (Vasan et al. 2022). They go by the names exogenous electrogenerators, anode-respiring bacteria, and electroactive bacteria as well. The electromagnetic transfer of electrons between bacteria is used by Microbial Fuel Cells (MFCs) to generate power for a range of applications (Logan 2009).

Cell respiration with solid metal oxidants, like iron, is the primary method by which bacterial strains transfer electrons from a ternary oxidase in the respiratory chain to furnish soluble Fe II outside the cell (Cheng et al. 2006; Vasan et al. 2022). Furthermore, *Methanothermobacter thermoautotrophicus* is an example of how cells may transfer electrons directly to one another without the need for intermediaries like hydrogen. It is electrically connected to *Peleomaculum thermopropionicum*

and allows for the transfer of electrons (Cheng et al. 2006). Furthermore, certain bacteria on an MFC's cathode—also known as a biocathode—catalyze oxygen reduction, which encourages bacterial growth by using electrons generated at the anode from the oxidation of organic materials (Logan and Regan 2006). The bacteria there receive energy from this process because electrons arrive at the biocathode at a voltage higher than that required for oxygen reduction.

The use of biocatalysts also made it possible to reduce nitrogen and hydrogen. It's becoming clearer that microbial fuel cell technology has a lot of potential as a sustainable energy source. Better implementation has been made possible by recent discoveries about the processes by which exoelectrogenic bacteria produce electrical current and on important aspects of MFC design (Logan and Regan 2006; Vasan et al. 2022). Although we know that bacteria in biofilms communicate with one another through quorum-sensing compounds, there is an unproven theory that suggests electron transfer may also play a role in cell-to-cell communication (Cheng et al. 2006).

*Pseudomonas aeruginosa* uses substances like acyl-HSLs to produce quorum signals, that are essential for bacterial communication (Gorby et al. 2006). P-coumaroyl-HSL, a substance produced by human and other animal neurons for cell-to-cell communication, is also produced by strains of *Rhodopseudomonas palustris* (Clauwaert et al. 2007). *P. aeruginosa* produces pyocyanin, which functions as an electron shutter in MFCs by generating an electrical current and detecting a cue that causes the upregulation of genes regulated by quorum sensing (Clauwaert et al. 2007).

As biosynthetic, bioenergetic, and signalling organelles, mitochondria are crucial to cellular physiology (Dietrich et al. 2006). Their malfunction can lead to a variety of age-related illnesses, from cancer to dementia. Cell death results from the removal of damaged mitochondria through pathways that are initiated by the loss of mitochondrial membrane potential (Rabaey et al. 2005). Cellular metabolism depends heavily on the tricarboxylic acid cycle flow, which generates molecules that feed into anabolic pathways and regulate biological outcomes including proliferation, differentiation, and adaptation (Chandel 2015). Cell destiny can be dictated by mitochondrial regulation of  $\text{Ca}^{2+}$ -dependent signaling cascades (Ashrafi and Schwarz 2013). The generation of ROS by mitochondria affects pathological and physiological processes related to ageing, cancer, and immunity.

#### Examples of electrogenic bacteria

Gram-negative bacteria transfer electrons in microbial fuel cells through specific mechanisms. Firstly, electrons need to be transported at the cell surface, posing

a challenge for Gram-negative bacteria due to the need for electron transfer across the cell membrane (White et al. 2016). These bacteria use bio-electrochemical frameworks that control the operation of microbial fuel cells; extracellular electron exchange is mostly mediated by Gram-negative bacteria like *Shewanella* and *Geobacter* species (Mahmoud et al. 2022). The process of electron transfer entails the movement of electrons from the cell wall to the electrodes, which is made possible by polypeptides that are absorbed on the surface of the bacterium (Roy et al. 2022). This efficient electron transfer mechanism is essential for the success of Gram-negative bacteria in microbial fuel cells, contributing to their high performance in bioenergy capture and power generation applications.

Gram-positive bacteria such as *Clostridium* and *Lactobacillus* species have shown promising results in microbial fuel cells, despite their less well-understood electron transfer mechanisms. Research indicates that Gram-positive bacteria, including *Enterococcus faecalis*, possess that capability for extracellular electron transfer, highlighting their potential in bio-electrochemical systems (Pankratova et al. 2018). Gram-positive bacteria isolated from microbial fuel cells demonstrated direct electron transfer, demonstrating their participation in electron exchange-activities essential to the creation of biofuel (Hubenova et al. 2022). Furthermore, it has been shown that, in the absence of cytochrome C, Gram-positive bacteria can absorb electrons through a series of membrane-bound complexes, providing more insight into the many methods these bacteria use to facilitate electron transfer in bio-electrochemical applications (Choi and Sang 2016). These findings underscore the importance of exploring and understanding the electron transfer mechanisms of Gram-positive bacteria to harness their full potential in microbial fuel cell technologies.

The structure of the cell walls of Gram-positive and Gram-negative bacteria differs; the former has a thick peptidoglycan layer and no outside lipid membrane, while the latter has both an outer lipid membrane and a thin peptidoglycan layer (Silhavy et al. 2010). Studies on Microbial Fuel Cells (MFC) have shown that both Gram-positive and Gram-negative bacteria are employed however, their efficacy in these systems exhibits variability. According to a study comparing the MFC power densities of Gram-positive and Gram-negative bacteria, the former have greater power densities than the latter (Juang et al. 2011). However, the choice of bacteria for MFC applications can depend on various factors, including the specific goals of the application and the characteristics of the wastewater used as a power source (Naha et al. 2023). While Gram-negative bacteria may show higher power densities in some studies, both Gram-positive and Gram-negative bacteria play essential roles in MFC technology,

each offering unique advantages based on the specific context of the applications.

### Utilizing electrogenic bacteria to enhance MFCs

Fundamental metrics used to evaluate the performance of electrogenic bacteria in MFCs are power density and coulombic efficiency, which indicate the ratio of electrons transmitted to the anode to the theoretical maximum. Certain types of microorganisms found in an MFC's anodic chamber and the system's overall architecture have a major impact on the power output and coulombic efficiency (Obileke et al. 2021). Furthermore, studies have shown that additions such as sodium citrate can increase MFC performance overall and power densities by improving power production, coulombic efficiency, and microbial community structure (Shanmuganathan et al. 2018). Understanding and optimizing these factors are essential for maximizing power output and coulombic efficiency in MFCs, thereby advancing bioelectricity generation capabilities and the efficiency of bio-electrochemical systems (Zhang et al. 2019).

Innovations such as air cathode MFCs have significantly improved power densities and coulombic efficiencies in the development of microbial fuel cell technology as compared to previous designs using aqueous cathodes (Logan et al. 2015). Furthermore, engineered bacteria have been utilized to enhance the maximum power density of mixed bacteria MFCs significantly, showcasing a notable increase in performance levels (Chen et al. 2021). To optimize microbial fuel cell topologies for greater power densities enhanced coulombic efficiencies and sustainable bioelectricity production, our findings highlight the significance of ongoing research and innovation (Cheng et al. 2006). By exploring factors that impact power density and coulombic efficiency, researchers can further enhance the performance of electrogenic bacteria in MFCs, contributing to the advancement of renewable energy technologies.

The effectiveness of electrogenic bacteria in MFCs depends on several variables, including power density, coulombic efficiency, substrate consumption, long-term stability, and tolerance to environmental challenges (Obileke et al. 2021). The significance of substrate utilization efficiency in maximizing power output and overall performance of MFCs, emphasises the importance of selecting bacteria with high substrate utilization rates for enhanced bioelectricity generation capabilities. Furthermore, long-term stability is essential for the sustained operation of MFCs, with research focusing on strategies to improve the durability and longevity of electrogenic bacteria within these systems to ensure consistent power production over extended periods (Greenman et al. 2021). The capacity to withstand environmental stressors, such as changes in temperature, pH,

and substrate availability, is also essential for the efficient functioning of MFCs since these stresses can affect the survival and performance of electrogenic bacteria in various settings (Roy et al. 2023).

Efforts to enhance the success of electrogenic bacteria in MFCs have involved exploring novel approaches such as biofilm formation and genetic engineering to improve substrate utilization efficiency, long-term stability, and stress resistance (Pandya et al. 2024). Biofilm formation has been shown to enhance electron transfer rates and overall MFC performance by promoting direct contact between bacteria and electrodes, leading to increased power densities and coulombic efficiencies (Connors et al. 2022). Genetic engineering techniques have also been employed to modify bacterial strains for improved substrate utilization capabilities and enhanced resistance to environmental stresses, further contributing to the success of electrogenic bacteria in microbial fuel cell applications (Zhou et al. 2023). By addressing factors like substrate utilization, long-term stability, and environmental stress resistance, researchers can advance the performance and reliability of electrogenic bacteria in MFCs, paving the way for more efficient bioelectricity generation technologies.

### Potential applications of microbial fuel cells

1. Treatment of wastewater and concurrent production of energy:

MFCs, have become a popular choice for treating wastewater and producing electricity at the same time. MFCs use the microbial breakdown of organic materials in wastewater to produce energy as a useful byproduct in addition to cleaning the water (Roy et al. 2023). MFCs' ability to treat wastewater while generating renewable energy demonstrates the technology's promise for environmentally friendly and productive wastewater treatment procedures.

The integration of wastewater treatment with energy generation in MFCs offers a synergistic approach to addressing environmental and energy challenges. This innovative technology not only contributes to cleaner water resources but also provides a renewable energy source, demonstrating the versatility and utility of MFCs in sustainable water treatment applications (Khandaker et al. 2021). The ability of MFCs to simultaneously treat wastewater and generate electricity underscores their potential as an environmentally friendly solution for wastewater management, offering a promising avenue for achieving both clean water and renewable energy goals (Jalili et al. 2024) (Table 3).

2. Powering remote or off-grid sensors and devices:



A potential method for the bioremediation of polluted settings is MFCs. By harnessing the metabolic activities of electrogenic bacteria, MFCs offer a sustainable approach to remediate polluted sites through microbial processes (Vinayak et al. 2021). The effectiveness of MFCs in degrading organic pollutants and facilitating the cleanup of contaminated environments demonstrates the potential of this technology for environmental remediation applications (Roy et al. 2023).

The unique ability of electrogenic bacteria in MFCs to break down contaminants while simultaneously generating electricity presents a dual benefit for environmental cleanup efforts. This dual functionality not only aids in the removal of pollutants but also contributes to renewable energy production, showcasing the versatility and efficiency of MFCs in addressing environmental challenges (Sonawane et al. 2022). The integration of bioremediation and energy generation in MFCs underscores their potential as a valuable tool for sustainable remediation practices, offering a holistic solution for cleaning up contaminated sites while harnessing clean energy resources (Pandya et al. 2024).

### 3. Bioremediation of contaminated environments:

The use of MFCs in the bioremediation of polluted settings has shown promise. By utilizing the metabolic activities of electrogenic bacteria, MFCs provide a sustainable approach to remediating polluted sites through

**Table 3** The primary potential uses of microbial fuel cells are outlined in this table, which also includes the use of MFC-based biosensors to monitor environmental pollutants, the bioremediation of contaminated environments, the powering of off-grid or remote sensors and devices, and wastewater treatment combined with energy generation. The chart offers a succinct summary of the various uses of MFC technology and emphasizes how adaptable it is for solving environmental issues and producing renewable energy

Application	Function
Wastewater Treatment and Energy Generation	MFCs offer a dual-purpose solution for treating wastewater while simultaneously generating renewable electricity from the microbial degradation of organic matter.
Powering Remote or Off-grid Sensors and Devices	The electricity generated by MFCs can be utilized to power remote or off-grid sensors and devices, providing a sustainable energy source in remote locations.
Bioremediation of Contaminated Environments	MFCs can facilitate the bioremediation of contaminated environments by utilising electrogenic bacteria to degrade organic pollutants while generating electricity.
Biosensors for Environmental Pollutant Monitoring	MFC-based biosensors can detect and quantify various environmental pollutants, such as heavy metals, organic compounds, and toxins, offering a sensitive and reliable method for environmental monitoring.

microbial processes (Vishwanathan 2021). The efficacy of MFCs in degrading organic pollutants and facilitating the cleanup of contaminated environments, showcases the potential of this technology for applications in environmental bioremediation (Borello et al. 2021).

The dual functionality of electrogenic bacteria in MFCs, enabling both contaminant degradation and electricity generation, offers a unique advantage for environmental cleanup efforts. This integrated approach not only aids in pollutant removal but also contributes to renewable energy production, highlighting the versatility and efficiency of MFCs in addressing environmental challenges (Sonawane et al. 2022). The ability of MFCs to combine bioremediation with energy generation underscores their potential as a valuable tool for sustainable remediation practices, providing a comprehensive solution for remediating contaminated sites while harnessing clean energy resources (Fang and Achal 2019).

### 4. Biosensors for monitoring environmental pollutants:

Biosensors utilizing MFCs have shown promise in monitoring environmental pollutants. By leveraging the electrogenic capabilities of bacteria within MFCs, these biosensors can detect and quantify various pollutants in the environment (Cui et al. 2019). The effectiveness of MFC-based biosensors in providing real-time monitoring of contaminants such as heavy metals, organic compounds, and toxins, offers a sensitive and reliable method for environmental pollutant detection (Huang et al. 2023).

By combining biosensors with MFC technology, pollution may be continuously and locally detected, offering a fresh method of environmental monitoring. MFC-based biosensors are useful instruments for environmental monitoring applications because of their benefits, which include high sensitivity, quick reaction times, and low detection limits (Zhai and Dong 2022). The use of microbial fuel cell biosensors holds great potential for enhancing pollution detection efforts, providing a cost-effective and sustainable solution for monitoring environmental pollutants in various ways (Jadhav et al. 2021) (Table 3).

### Optimal conditions for electrogenic bacteria

#### 1. Neutral to slightly alkaline pH:

Maintaining a neutral to slightly alkaline pH environment is crucial for the optimal performance of electrogenic bacteria in MFCs. Research studies have highlighted the importance of pH control in MFC systems, as it directly impacts the activity and growth of electrogenic bacteria (Bagchi and Behera 2021). The significance of maintaining a pH range between 7 and 9 for efficient electron

transfer processes and enhanced power generation in MFCs. This neutral to slightly alkaline pH range provides an ideal environment for electrogenic bacteria to thrive and facilitate effective electron transfer mechanisms, ultimately improving the overall performance of microbial fuel cells (De La Cruz-Noriega et al. 2023).

The influence of pH on electrogenic bacteria in MFCs extends beyond their metabolic activities to impact biofilm formation, substrate utilization, and overall system efficiency (Mahmoud et al. 2022). The variations in pH levels can affect the composition and structure of microbial communities within MFCs, influencing their ability to generate electricity from organic matter. To improve the development and activity of electrogenic bacteria and their effectiveness in bioelectricity-generating applications, researchers can optimize the pH conditions within MFCs to maintain a neutral to slightly alkaline range (Sonawane et al. 2022). This emphasis on pH control underscores its critical role in maximizing the efficiency and effectiveness of microbial fuel cells for sustainable energy production (Table 4).

#### 2. Anaerobic or microaerobic conditions:

Maintaining anaerobic or microaerobic conditions is essential for the optimal function of electrogenic bacteria in MFCs. Anaerobic conditions in the MFC anode compartment have been demonstrated to promote the development and activity of bacteria participating in electron transfer activities (Tahernia et al. 2020). The importance of anaerobic conditions for efficient electron generation and enhanced power output in MFCs. Additionally, membrane-less MFCs can utilize anaerobic bacteria even in aerobic environments, emphasizing the adaptability of electrogenic bacteria to different oxygen levels within microbial fuel cell systems (Gupta et al. 2023).

The utilization of anaerobic oxidation processes by electrogenic bacteria in MFCs plays a crucial role in bioelectricity generation. By harnessing active microorganisms under anaerobic conditions, MFCs can effectively degrade pollutants and produce electrons through microbial metabolism. This strategy shows the promise for sustainable energy conversion systems that include bacterial biofilms in electrochemical environments, as shown in microbial fuel cell technology (Pandya et al. 2024). The ability of electrogenic bacteria to thrive and function optimally under anaerobic or microaerobic conditions underscores their significance in driving bioelectricity generation processes within microbial fuel cells, highlighting the importance of maintaining specific oxygen levels to support their metabolic activities (Greenman et al. 2021).

#### 3. Availability of suitable electron donors (e.g., organic compounds, hydrogen):

For electrogenic bacteria in MFCs to work as best they can, appropriate electron donors such as hydrogen and organic molecules must be available. The electrogenic bacteria select electrodes as preferred electron acceptors in bio-electrochemical systems due to the potential energy benefits derived from this interaction (Roy et al. 2022). The development of bacteria that are electrogenic in the presence of electron donors, such as lactate, since these substances are necessary for their metabolic processes. This utilisation of organic compounds as electron donors, coupled with electrodes as electron acceptors, highlights the importance of providing suitable electron sources to support the growth and activity of electrogenic bacteria within MFCs (Sacco et al. 2017).

The ability of electrogenic bacteria to utilise various electron donors, including organic compounds and hydrogen, underscores their versatility in bioelectricity generation processes (Choi 2022). To extract live electrogenic bacteria and demonstrate their capacity to adapt to various electron acceptors, enrichment broths containing insoluble  $\text{Fe}^{+3}$ -oxides have been employed. The prioritization and availability of carbon sources play a significant role in limiting bidirectional electron transfer processes within microbial fuel cells (Rumora et al. 2023). By understanding and optimising the availability of suitable electron donors, researchers can enhance the performance and efficiency of electrogenic bacteria in MFCs, ultimately improving bioelectricity generation capabilities and advancing sustainable energy conversion technologies (Michalska et al. 2023).

#### 4. Presence of electron shuttles or conductive materials to facilitate electron transfer:

The presence of electron shuttles or conductive materials plays a vital role in facilitating electron transfer with electrogenic bacteria in MFCs. Electron shuttles, such as quinones and humic substances, can enhance extracellular electron transfer by shuttling electrons between bacteria and electrodes. The efficiency of producing bioelectricity in MFCs is enhanced by the ability of conductive materials such as graphene and carbon nanotubes to facilitate direct electron transmission between electrogenic bacteria and electrodes (Hazzan et al. 2023). The utilization of electron shuttles or conductive materials provides alternative pathways for electron transfer, enabling electrogenic bacteria to efficiently transfer electrons to external acceptors, thereby enhancing the overall performance of microbial fuel cell systems (Slate et al. 2019).

The use of conductive materials or electron shuttles in MFCs provides creative ways to improve power

production and optimize electron transfer processes. By utilizing redox mediators or conductive materials, researchers can improve the efficiency of electron exchange mechanisms between electrogenic bacteria and electrodes. The presence of electron shuttles or conductive materials not only facilitates electron transfer but also promotes biofilm formation and enhances the stability of microbial communities within MFCs (Conners et al. 2022). These advancements in bio-electrochemical systems underscore the importance of leveraging electron shuttles or conductive materials to create conducive environments for electrogenic bacteria, ultimately leading to improved bioelectricity generation capabilities and the development of sustainable energy conversion technologies (Zheng et al. 2020) (Table 4).

#### Exclusion of archaea

While some archaea exhibit electrogenic properties, the majority of research on MFCs has predominantly focused on bacteria. This emphasis on bacteria is attributed to their higher abundance and better-understood electron transfer mechanisms compared to archaea, leading to a more comprehensive understanding of bacterial involvement in bioelectricity generation (Abrevaya et al. 2011). The prevalence of bacteria in MFC research is due to their well-established roles in extracellular electron transfer processes, which are essential for efficient energy conversion within microbial fuel cell systems (Jiang et al. 2018).

The exclusion of archaea from extensive research on microbial fuel cells is primarily driven by the abundance

**Table 4** This table summarizes the key optimal conditions for electrogenic bacteria in MFCs, including the pH range, oxygen level, availability of suitable electron donors, and the presence of electron shuttles or conductive materials to facilitate electron transfer processes. The table provides a concise overview of the factors that contribute to the optimal performance of electrogenic bacteria in MFC systems

Optimal Condition	Function
pH	Neutral to slightly alkaline pH (range of 7 to 9) provides an ideal environment for efficient electron transfer processes and enhanced power generation.
Oxygen Level	Electrogenic bacteria that are engaged in electron transfer activities develop and are supported in the anode compartment by anaerobic or microaerobic conditions.
Electron Donors	The availability of suitable electron donors, such as organic compounds (e.g., lactate) and hydrogen, is crucial for the metabolic activities and growth of electrogenic bacteria.
Electron Shuttles/ Conductive Materials	The presence of electron shuttles (e.g., quinones, humic substances) or conductive materials (e.g., carbon nanotubes, graphene) facilitates extracellular electron transfer between bacteria and electrodes, improving bioelectricity generation

and well-characterized electron transfer mechanisms of bacteria. While some archaea demonstrate electrogenic properties, the prevalence and understanding of bacterial involvement in electron transfer processes have positioned them as the primary subjects of MFC investigations (Garbini et al. 2023). The utilization of bacteria in MFCs for pollutant degradation and bioelectricity generation highlights their significance in sustainable energy technologies. The potential exhibited by archaea microorganisms like *Haloferax volcanii* and *Natrialba magadii*, the focus on bacteria in MFC research reflects a strategic approach to leveraging well-established knowledge and mechanisms for optimizing bioelectrochemical systems and advancing renewable energy applications (Nevin et al. 2008).

*Geoglobus* and *Ferroglobus* species exhibit unique electron transfer pathways that enable them to participate in bioelectricity generation processes. *Geoglobus acetivorans*, a member of the *Geoglobus* genus, is known for its Fe(III) reduction capabilities and acetate metabolism, showcasing distinct electron transfer processes that contribute to its electrogenic activity (Mardanov et al. 2015). These species grow autotrophically by hydrogen oxidation and are obligately dependent on Fe(III)-citrate or ferrihydrite as terminal electron acceptors, highlighting their specialized electron transfer mechanisms in utilizing iron compounds for energy generation. In pure cultures, *Ferroglobus placidus* and *Geoglobus ahangari* have demonstrated the ability to generate electricity in microbial fuel cells at high temperatures, indicating their unique exoelectrogenic properties and involvement in electron transfer pathways for bioelectricity production (Sekar et al. 2017).

The archaeon of *hyperthermophilic*, *Ferroglobus placidus* demonstrates its versatility in bioelectricity-generating processes by employing a broad range of electron donors, including hydrocarbons and aromatic chemicals, to demonstrate its varied electron transfer capabilities (Smith et al. 2015). *Ferroglobus placidus* possesses a large number of ferredoxins and Fe-S binding domain proteins in its genome. These proteins are crucial for electron transfer pathways and are important for enabling effective electron exchange processes in microbial fuel cells (Manzella et al. 2015). These findings highlight the diverse and specialized electron transfer pathways of *Geoglobus* and *Ferroglobus* species, underscoring their potential contributions.

#### Mitophagy

Mitophagy, the selective breakdown of mitochondria, affects cellular energy metabolism and homeostasis, which can have a substantial effect on the functionality of eukaryotic MFCs. The mitophagy pathways are essential for maintaining mitochondrial quality control and

clearance, which are crucial for the efficient turnover of dysfunctional mitochondria in eukaryotic microorganisms like yeast and algae within MFCs (Ashrafi and Schwarz 2013). By regulating mitophagy, eukaryotic cells can optimize their bioenergetic efficiency and electron transfer processes, ultimately affecting the overall performance of microbial fuel cells (Ma et al. 2020).

To comprehend how mitophagy impacts eukaryotic MFCs, it is especially important to consider the interaction between mitochondrial biogenesis and mitophagy. In other circumstances, inhibiting mitophagy may not considerably enhance particular processes, such as *Saccharomyces cerevisiae*'s synthesis of fuel ethanol (Eliodório et al. 2022). The broader implications of mitophagy on cellular quality control and energy metabolism are crucial for the bio-electrochemical activity of eukaryotic microorganisms in MFCs. Mitophagy pathways indirectly affect the bioenergetic efficiency and electron transfer mechanisms that are essential for the production of electricity in microbial fuel cells by helping to maintain cellular homeostasis and energy balance (Ding and Yin 2012).

## Conclusion

To conclude, this review illuminates the intricate parallels and distinct characteristics between mitochondrial and bacterial electron transport chains, revealing the fundamental mechanisms that underpin energy synthesis in cells. By exploring the evolutionary convergence of these pathways, we gain insights into the shared bioenergetic strategies that have been optimized across different life forms. Moreover, using these concepts in MFCs offers a viable path toward the production of sustainable energy by utilizing the inherent competence of electrogenic bacteria in electron transfer activities. This review not only advances our understanding of cellular energy mechanisms but also highlights the potential of bio-engineering and synthetic biology in creating efficient, renewable energy solutions. Through the exploration of optimal conditions for electrogenic bacteria, including pH balance, anaerobic environments, and the provision of suitable electron donors, we can enhance MFC performance, underscoring the significance of this technology in addressing global energy challenges. Furthermore, the study of mitophagy within the framework of eukaryotic MFCs raises the possibility of an indirect involvement in promoting electrogenic bacteria's optimum performance, underscoring the intricate relationship between cellular functions and the production of bioelectricity. This work paves the way for future research aimed at harnessing the power of bioenergetics for environmental and technological advancements.

## Abbreviations

ADP	Adenosine Diphosphate
AMP	Adenosine Monophosphate

ATP	Adenosine Triphosphate
FADH <sub>2</sub>	Flavin Adenine Dinucleotide
GTP	Guanosine Triphosphate
MFC	Microbial Fuel Cell
NADH	Nicotinamide Adenine Dinucleotide (NAD) + Hydrogen (H)
ROS	Reactive Oxygen Species

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## Author contributions

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