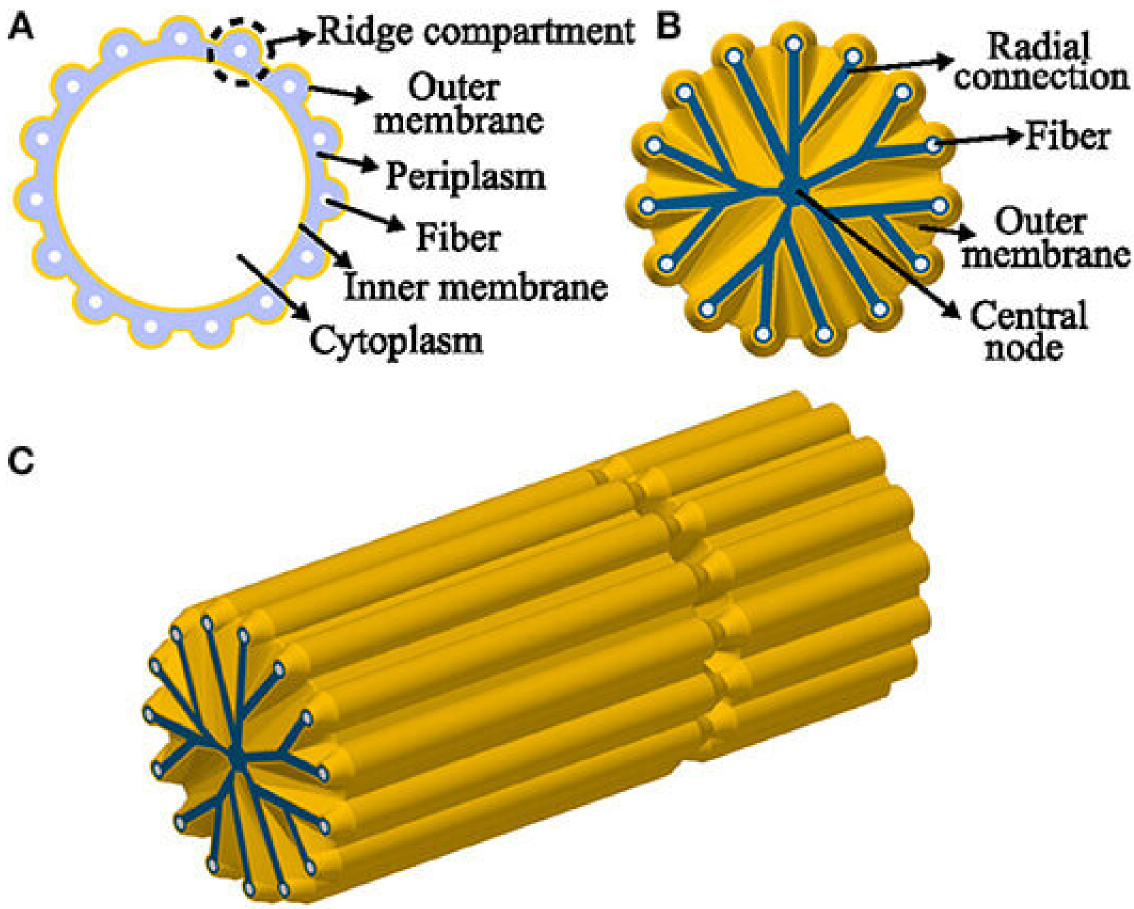
Cable bacteria: Electric marvels of microbial world

July 19 2022, by Kartik Aiyer



Schematic representation of cable bacteria. A: Cross-section of a cable bacterium cell; B: transverse cross-section at a junction; C: a 3-D view of a cell, connected. Credit: [Wikimedia Commons]

The emergence of multicellularity, requiring complex interactions between different groups of individual cells for metabolic and physiological benefits, is a great success in the history of biology. While multicellularity is commonly associated with eukaryotes, the relatively recent discovery of multicellular bacteria in sediments has added perplexity to the nature and organization of these cells. Remarkably, the interactions in this group of bacteria, known as cable bacteria, occur via electricity.

Cable bacteria structure and metabolism

Cable bacteria are multicellular, filamentous bacteria present ubiquitously in both freshwater and marine sediments. Known to form filaments up to a few centimeters in length, cable bacteria consist of long, unbranched sets of cells, which are vertically oriented in the sediments. Cells within a cable are interconnected at the cell- junctions, and a series of ridges are present across the length of the filaments. Owing to their motile nature, cable bacteria align themselves along vertical redox gradients present in the water-sediment interface.

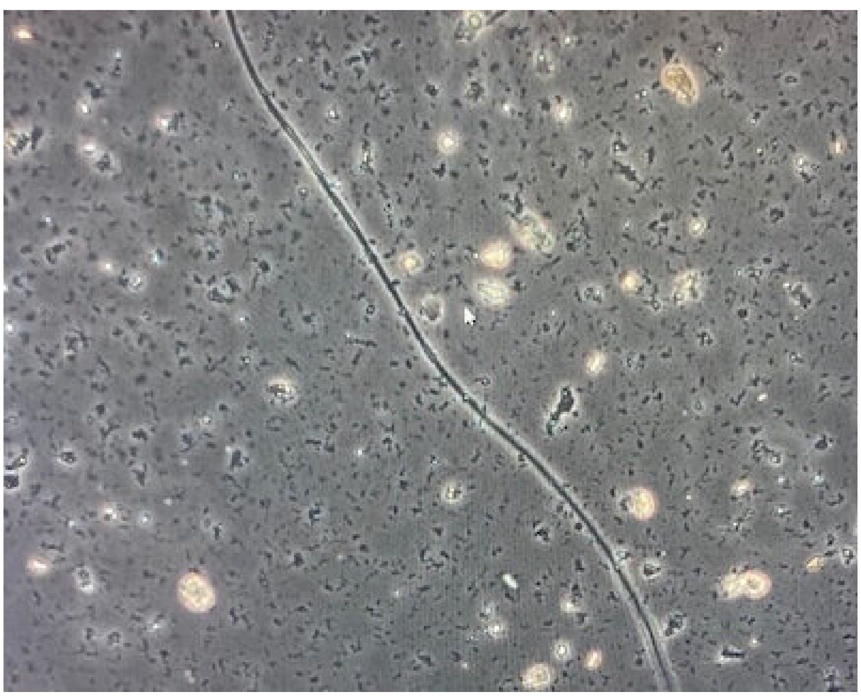
They are unique in their ability to divide metabolic labor among different cells of the cable. In other words, while some of the cells buried in the anoxic sediment generate energy by oxidizing an electron donor (most commonly sulfide), other cells reduce oxygen at the oxic zone performing a different redox-half reaction. This type of metabolic behavior certainly does not conform to the longstanding dogma in biology that every individual living cell independently generates its own energy supply.

Mechanism of long-distance electron transport (LDET)

Equally remarkable, the separation of half-reactions among different cells in the cable is made possible due to [long-distance electron transfer (LDET)](), which facilitates conduction of electrons generated by sulfide oxidation in the anoxic sediment all the way across the cable to reduce oxygen. This mechanism ensures that cells separated over long distances are still capable of participating in a single metabolic redox reaction.

LDET may occur over distances as long as 2–3 cm, a humongous distance for a microbe.

How is this possible? After oxidation, electrons are channeled into the periplasm, where they are transferred by cytochromes onto conductive filaments containing e-pili (electrically conductive pili), which are composed of aromatic amino acids and enable LDET. Notably, e-pili are also present in conventional electroactive bacteria like Geobacter and have been implicated in extracellular electron transfer to electrodes in [bioelectrochemical systems]().



Microscopy image of a cable bacterium; scale bar 10μm. Credit: Kartik Aiyer, After LDET occurs, the electrons are offloaded directly to final electron acceptors like oxygen and nitrate. An interesting feature in this metabolic pathway is that energy conservation occurs only in the sulfide-oxidizing cells present in the anoxic sediment, and not in the oxygen-reducing cells. The phenomenon of mining sulfides deeper in the sediment and transporting the electrons to reduce oxygen provides a competitive advantage to cable bacteria, as they can utilize the redox gradients to outperform other local sulfur oxidizing bacteria.

Techniques, including scanning transmission electron microscopy –energy-dispersive X-ray spectroscopy (STEM-EDX), confocal Raman microscopy and stable isotope labeling, have further revealed that the periplasmic wires of cable bacteria possess a conductive protein core that relies on nickel as a coenzyme. Selective removal or oxidation of nickel significantly decreased conductivity of cable bacteria fibers. The involvement of nickel in the conductive pathway is unlike any other mechanism of electron transport, since iron is the principal component of conductive protein nanowires present in Geobacter.

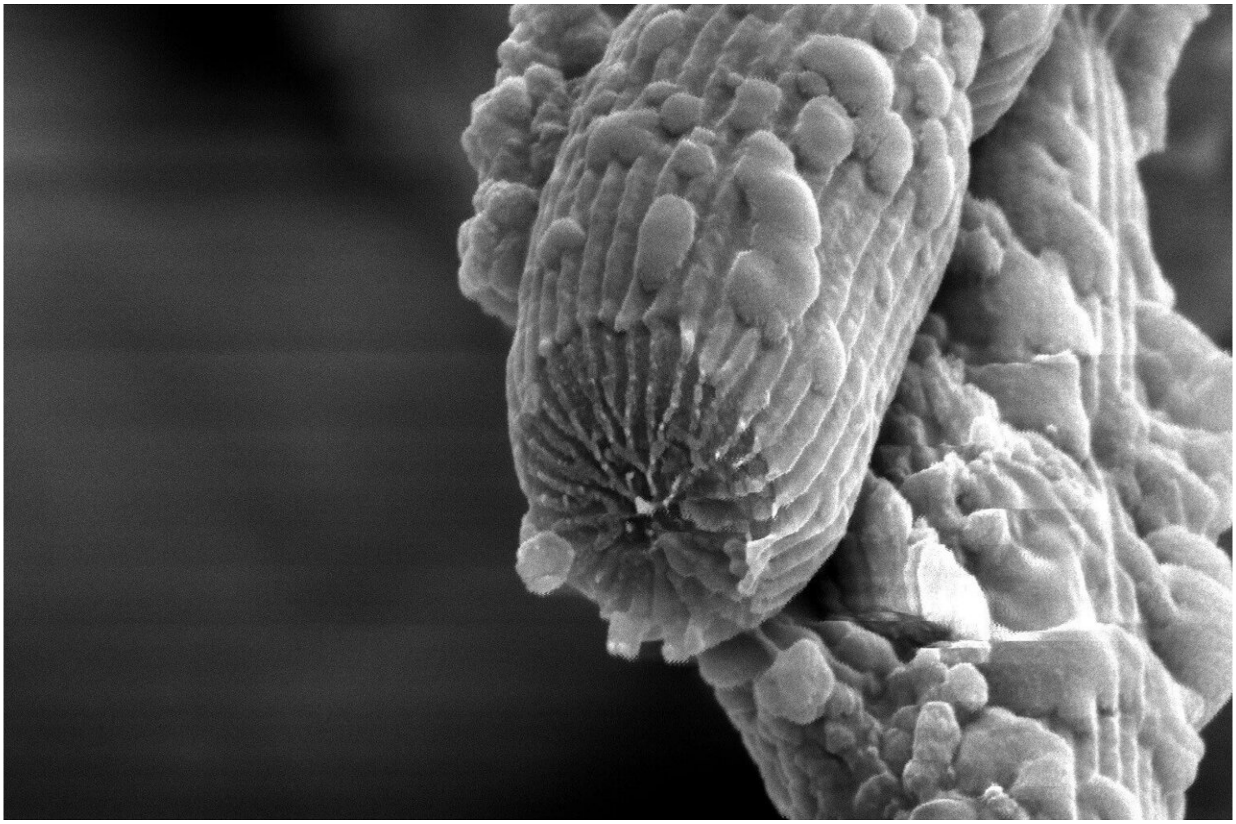
Potential applications

While LDET has been confirmed experimentally, other metabolic features of cable bacteria have only been indirectly deduced, owing to disappearance of potential substrates and the presence of metabolites in sediments. Furthermore, a comprehensive understanding of the inter and intra-cellular electron transport is currently lacking, which presents an exciting field of research.

Since much is left to be understood about several fundamental aspects of cable bacteria, relatively few applications have been conceived. However, even a cursory glance at these fascinating microbes is sufficient to conclude that they will likely have several useful applications in the future. For example:

- Cable bacteria were found to be associated with the roots of aquatic plants, such as the rice plant (Oryza sativa). This plant-cable bacteria relationship could mitigate sulfide toxicity in rice plants and seagrass meadows.
- Cable bacteria are also important players in biogeochemical cycling, as they may acidify their immediate surroundings, thereby mobilizing essential plant nutrients like phosphates and iron.
- Cable bacteria could also potentially help in nitrogen fixation, which may eventually lead to generation of ammonia and subsequently improve the nitrogen availability to plants.
- In rice-vegetated soils, inoculation of cable bacteria leads to a significant decrease in methane emissions, since cable bacteria compete with methanogens for the same substrates.

The conductive fiber sheaths from cable bacteria could also potentially serve as biomaterials for designing electronic components and could be an excellent candidate for the development of biodegradable electronics, to reduce e-waste. While nanowires from electroactive bacteria like Geobacter are also being considered for the same purpose, their main limitation stems from the fact that only short-distance electron transfer can be achieved with such nanowires. Cable bacteria, on the other hand, have successfully transcended the micrometer conduction range and can effectively participate in long-range electron transfer, which could prove very useful in designing electronic components. Direct current and alternating current signals were successfully shown to pass through the conductive filaments of cable bacteria. Interestingly, cable bacteria were also demonstrated to work as transistors, making them relevant in designing computational circuits.



SEM image of a cable bacterium cell. Credit: Kartik Aiyer, American Society for Microbiology

Discovery of cable bacteria

The discovery of cable bacteria occurred relatively recently, around a decade ago. Microbiologist Lars Peter Nielsen from Aarhus University in Denmark was studying sediments collected from the Aarhus Harbor. Initially, the sediments were stinky and saturated with hydrogen sulfide. However, in a span of weeks, they turned paler and demonstrated a drop in sulfide levels. This observation proved mysterious, since no geochemical process were known to result in depletion of sulfide.

Further, the researchers detected an electrical current through the mud. Since metallic shuttling of electrons was ruled out as a possibility, the only plausible source of these observations seemed to be a biological entity that consumed sulfide to liberate electrons. Upon closer examination of the sediments using electron microscopy, the suspect was identified: thin, long, bacterial filaments consisting of stacks of cells. The name "cable bacteria" was inspired by the structure of bacterial filaments, which resembled long cables.

16S rRNA sequencing, placed cable bacteria in the Deltaproteobacteria family Desulfobulbaceae. This family also contains several other sulfate-reducing and aerobic sulfide-oxidizing microbes. The cable bacteria clade consists of the genera Candidatus Electrothrix, a marine cable bacterium, and Candidatus Electronema, a freshwater cable bacterium. Cable bacteria have not yet been isolated in pure culture; though freshwater cable bacteria have been selectively enriched via agar pillar gradient columns. Unsurprisingly, cable bacteria genomes show similarities with those of sulfate-reducing bacteria, however, they are classified as mixotrophs and chemolithoautotrophs that can oxidize sulfide by potentially reversing the sulfate reduction pathway.

Provided by American Society for Microbiology

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