Opinion

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Discovery of giant bacteria: do we need to change the definition of microorganisms?

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Introduction

By definition, bacteria are prokaryotic microorganisms i.e. unicellular living organisms lacking intracellular membrane-bound compartments and too small to be visible to the naked eye. However, some types of bacteria, belonging to a few bacterial phyla, visible without the aid of microscopes, have been discovered in the past four decades. One of the earliest so-called 'giant bacteria' was discovered in 1985 as a gut symbiont of brown surgeonfish (*Acanthurus nigrofuscus*) by a team led by Lev Fishelson.[1] This organism is cigar-shaped and ranged in length from 10 to 600 µm. The largest cigar-shaped cells are definitely big enough to be visible to the naked human eye. This organism was called *Epulopiscium fishelsoni* which was definitely established to be bacteria belonging to the phylum Firmicutes through numerous studies. The name '*Epulopiscium*' literally means 'guest at a banquet of a fish.' This discovery raised the perplexing issue of whether some bacteria are 'macro microbes' or 'giant bacteria' and if there is a need to modify the definition of microorganisms as "living beings too small to be seen without the help of a microscope." It also triggered several other questions: how movement of molecules are ensured within the immensely increased cellular volume, how the cell membrane is organized, whether the DNA is organized like that in other normal bacteria, how do the metabolism and division in such giant bacteria differ from that of average bacteria.

Another giant bacterium, *Thiomargarita namibiensis*, was discovered in 1999 from sediments off the continental shelf of Namibia.[2] *Thiomargarita* literally means 'sulfur pearl.' The cells have mean diameters of 100-300 µm but large cells can measure up to 800 µm. The active cytoplasm is restricted to a thin outer layer of about 0.5 to 2 µm. There is a giant central vacuole that stores high concentrations of nitrate (used as electron acceptor to oxidize S compounds, which are electron donors).

The current record-holder among giant bacteria is *Thiomargarita magnifica* which was originally discovered by Oliver Gros in the early 2010s from mangroves in the Guadeloupe archipelago in French Antilles.[3] This bacterium belongs to the phylum Gamma proteo bacteria. For a long time, it was thought to be a fungus. Later, it was established to be a bacterium which is filamentous with average cell length of 10 mm; with larger individuals often measuring up to 20 mm. The unusual structural and functional properties of *T. magnifica* have now been worked out by the team led by Jean-Marie Volland, research student supervised by Gros.[3]

Another member of the *Epulopiscium* family, *E. viviparus*, has now been discovered and its unique properties have been published.[4] *Epulopiscium* spp. is large, motile microbes. Initially, they were considered to be a new kind of microbial eukaryote. However, molecular studies including 16S rDNA analyses established them to be bacteria. Most of them are found as intestinal symbionts of sturgeon fish in tropical reef ecosystems e.g. Great Barrier Reef, Hawaii, Guam and other locations in the Pacific and Atlantic oceans. Individual cells may reach up to 600 µm in length and 80 µm in width.

Let us now briefly consider the unique structural and biochemical, and physiological properties of giant bacteria.

As bacterial sizes increase, the surface area does not increase in step with the rise in cell volume. Bacteria depend on diffusion for transport of substances from the environment into the cell as well as for intracellular trafficking. The larger the cell, the smaller is the surface area-to-volume ratio. For example, this value drops from 6 for a spherical cell with a diameter of 1 um to 0.6 and 0.06 for a cell with a diameter of 10 or 100 um respectively.[5–7] This may affect the metabolic rate of the bacteria. How do these large bacteria solve this problem? *Epulopiscium* spp. has highly folded cell membranes enabling the increase in cell surface area. *T magnifica* has membrane-bound sacs called pepins that contain DNA and ribosomes.[8] This makes it possible to carry out localized synthesis of proteins and other cellular molecules without the need for molecules traveling long distances. Also, the presence of a large central vacuole pushes the cytoplasm at the periphery of the large cell, further obviating the need for molecules to be transported over long distances.

Also, many of these giant bacteria have multiple copies of the genome enabling localized RNA and protein synthesis. Reproduction and cell division are also quite unique in these giant bacteria. *E. fishelsoni* and other *Epulopiscium* species seem to develop internal offspring and deliver these "baby bacteria" as daughter bacteria. *T. namibiensis* seems to reproduce by fission. But *T. magnifica* has some unique properties. It possibly reproduces by some form of asymmetric fission. The parent cell does not split into two daughter cells of equal size. This seems like reproduction by budding-the kind found in yeasts.

The most amazing things about *T. magnifica* are its enormous DNA content. Its genome is about 12 million base pairs (three times that of an average bacterium).[9] And, unlike other bacteria, which have DNA floating around in the cytoplasm, its DNA is kept in membrane-bound sacs called pepins that house both DNA and ribosomes. There are about 5,00,000 pepins in a single cell. So, a *Thiomargarita* *magnifica* cell has trillions of base pairs of DNA (total DNA content is even larger than the human genome). And, a large part of this DNA is devoted to synthesis of secondary metabolites such as antibiotics to ward off other microbial predators.[9]

Thus, macroscopic bacteria seem to solve the problem of diffusional limitation in giant cells by increasing the in foldings of the plasma membrane, having a central vacuole that pushes cytoplasm to a narrow cell periphery, keeping multiple copies of a polypoid genome in organelle-like structures called pepins, enabling localized RNA and protein synthesis etc.

The years ahead seem to be quite exciting. Many more giant bacteria may be lurking round in the various terrestrial and marine ecosystems of the world or as symbionts of fishes and other plant and animal hosts. Who knows some of these yet-to-be-discovered 'macroscopic bacteria' (giant bacteria) may be the connecting link between the prokaryotic and eukaryotic organisms?

As certain bacteria are visible to the human eye, have membrane-bound sacs, and polyploid DNA in organelle-like structures; we need to ponder if we need to change our textbooks to accommodate these macro microbes and/or if we need to change the very definition of a microorganism or a bacterium?

Now, the boundary between eukaryotes and prokaryotes has become blurred.[10] The classic definition of bacteria is microscopic single-celled organisms which are prokaryotic, i.e. they lack membrane-bound nucleus and other membrane-enclosed organelles. Many recently-discovered giant bacteria are visible to the human eye (macroscopic microbes) and some of them e.g. *T. magnifica* have polyploid genomes enclosed in membrane-bound sacs called pepins (not a single genome floating around in the cytoplasm), besides a membrane-enclosed central vacuole. Thus, macro bacteria such as *T. magnifica* are neither microscopic nor strictly prokaryotic as they have DNA enclosed in pepins and organelle-like central vacuole. It is quite possible that many more missing links between prokaryotes and eukaryotes may be lurking in the world's oceans and other ecosystems.

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None.

Conflicts of interest

The author declares that there are no conflicts of interest.

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