Micron 39 (2008) 1387–1392

Contents lists available at ScienceDirect

Micron

journal homepage: www.elsevier.com/locate/micron

Short communication

Ultrastructure and cytochemistry of lipid granules in the many-celled magnetotactic prokaryote, '*Candidatus* Magnetoglobus multicellularis'

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ARTICLE INFO

Article history:
Received 18 March 2008
Received in revised form 25 May 2008
Accepted 26 May 2008

Keywords:
Cytochemistry
Lipid granules
Lipid ultrastructure
Magnetotactic bacteria
Magnetotactic multicellular prokaryotes
Polyhydroxyalkanoates

ABSTRACT

Conspicuous cytoplasmic granules are reported in a magnetotactic multicellular prokaryote named '*Candidatus* Magnetoglobus multicellularis'. Unfortunately, this microorganism, which consists of an assembly of gram-negative bacterial cells, cannot yet be cultivated, limiting the biochemical analysis of the granules and preventing *in vitro* studies with starvation/excess of nutrients. In this scenario, light and electron microscopy techniques were used to partially address the nature of the granules. Besides magnetosomes, three types of inclusions were observed: small (mean diameter = 124 nm) polyhydroxyalkanoate-like (PHA) granules, large (diameters ranging from 0.11 to 2.5 μm) non-PHA lipid granules, and rare phosphorus-rich granules, which probably correspond to polyphosphate bodies. The PHA granules were rounded in projection, non-reactive with OsO_4, and suffered the typical plastic deformation of PHAs after freeze fracturing. The nature of the large granules, consisting of round globular structures (mean diameter = 0.76 μm), was classified as non-PHA based on the following data: (a) multilayered structure in freeze-fracture electron microscopy, typical of non-PHA lipids; (b) Nile blue fluorescence imaging detected non-PHA lipids; (c) imidazole buffered osmium tetroxide and ruthenium red cytochemistry stained the globules, which appeared as electron-dense granules instead of electron lucent as PHAs do. Most likely, '*Candidatus* Magnetoglobus multicellularis' stores carbon mainly as unusual lipid granules, together with smaller amounts of PHAs.

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1. Introduction

Bacteria, propelled by flagella that are capable of aligning and migrating along magnetic field lines are called magnetotactic bacteria. All magnetotactic bacteria produce intracellular magnetic organelles, called magnetosomes, responsible for their magnetic orientation. Each magnetosome comprises a crystalline phase (magnetite, Fe_3O_4 or greigite, Fe_3S_4) enveloped by a true membrane in cultivated species (Komeili et al., 2006) or, possibly, a matrix or protein envelope in uncultivated species (Hanzlik et al., 2002; Taylor and Barry, 2004). Intracellular granules, other than magnetosomes, have been described in many uncultured magnetotactic bacteria (Keim et al., 2005). Phosphorus-rich granules are common in both marine (Lins and Farina, 1999; Keim et al., 2001, 2005) and freshwater magnetotactic cocci (Cox et al., 2002), where they usually occur as two large cytoplasmic globules. Polyhydroxyalkanoate (PHA) granules have been observed in the cultivated species *Magnetospirillum magnetotacticum* (Gorby et al., 1988; Martins et al., 2007). Sulfur inclusions have been reported in uncultured magnetotactic bacteria including *Magnetobacterium bavaricum* (Spring et al., 1993), *Bilophococcus magnetotacticum* (Moench, 1988), and others (Cox et al., 2002; Keim et al., 2001, 2005). In cultivated species including vibrioid strains (MV-1 and MV-2), coccus strain MC-1, and spirillum strain MV-4, cells are capable of chemolithoautotrophic growth by oxidation of sulfur compounds with the intermediate accumulation of sulfur inclusions (Bazylinski and Frankel, 2004).

Magnetotactic bacteria are morphologically diverse and include cocci, spirilla, rods and many-celled magnetotactic prokaryotes (MMP). MMPs occur in many anoxic environments around the world (Keim et al., 2007). '*Candidatus* Magnetoglobus multicellularis' (Abreu et al., 2007) is the best-characterized MMP (Keim et al., 2004a,b; Abreu et al., 2006, 2007; Silva et al., 2007; Winklhofer et al., 2007). In this microorganism, about 20 gram-negative bacterial cells are organized around a central region in a

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doi:10.1016/j.micron.2008.05.009

spherical assembly that collectively swims as a unit, forming a unique morphology among prokaryotes. Each cell contains iron sulfide magnetosomes that are organized in planar groups within the cells, imparting to the whole microorganism a net magnetic moment (Keim et al., 2007). The surface of each cell is covered with about 30 flagella (Silva et al., 2007) that collectively propel the microorganism within the sediment towards a suitable environment. Conspicuous intracellular granules are observed in '*Candidatus* Magnetoglobus multicellularis' cells (Keim et al., 2004a; Abreu et al., 2007), and also in other MMPs (Rodgers et al., 1990; Lins et al., 2007), but no systematic study has been done on them. Unfortunately, this microorganism cannot yet be cultivated, limiting the analysis of the granules by biochemistry and preventing *in vitro* studies with starvation/excess of nutrients.

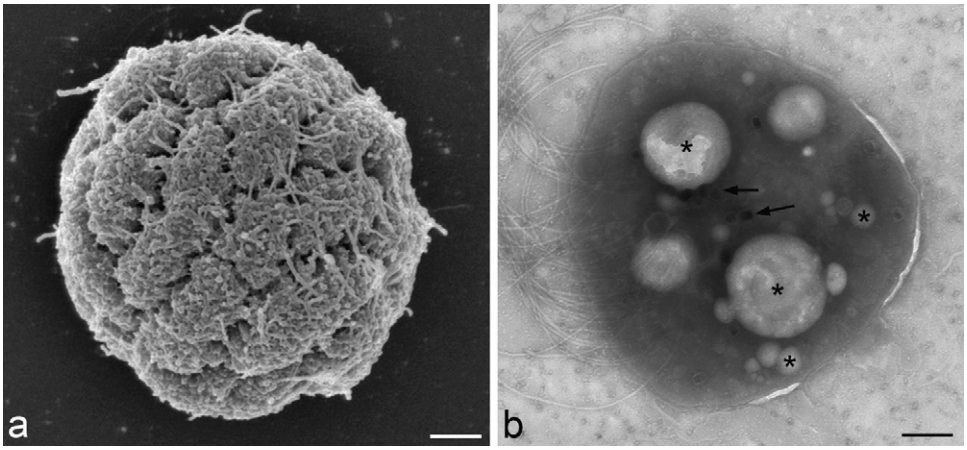

Fig. 1. Morphology of '*Candidatus* Magnetoglobus multicellularis'. (a) Scanning electron microscopy image showing the surface morphology of the microorganism. (b) Whole mount of a cell showing magnetosomes (arrows) and granules (asterisks). Bar = 500 nm for (a) and 300 nm for (b).

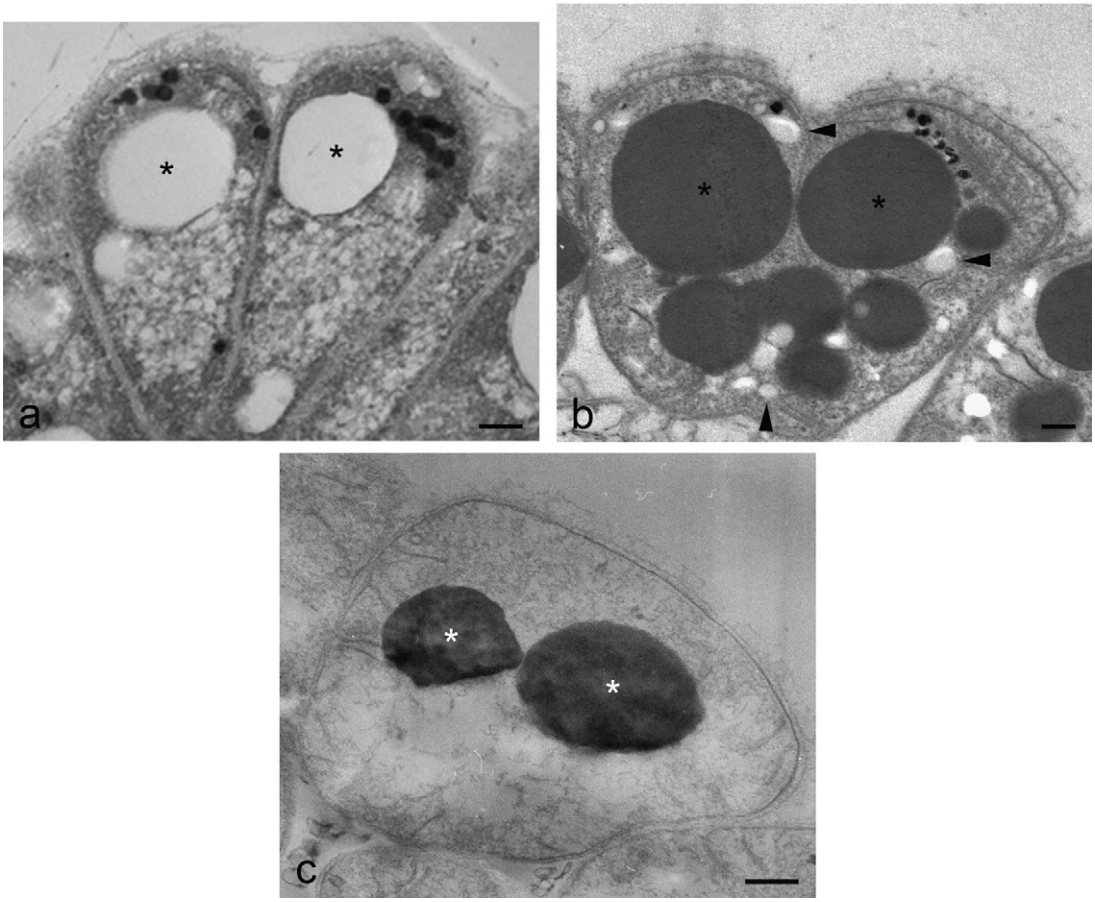

Fig. 2. Ultra-thin sections of the cells of '*Candidatus* Magnetoglobus multicellularis' showing the lipid granules. The small electron-dense structures are the magnetosomes. (a) An ultra-thin section of a microorganism, which was not post-fixed with OsO_4, showing large electron lucent granules (asterisks). (b) Sample prepared with ruthenium red, showing large stained granules (asterisks) and smaller electron-lucent granules (arrowheads). (c) Imidazole buffered osmium tetroxide cytochemistry of '*Candidatus* Magnetoglobus multicellularis.' Note the two highly electron-dense (asterisks) granules within the cell. Bars = 200 nm.

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