DIVERSITY OF FORM, FUNCTION AND ADAPTATION IN MICROORGANISMS

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Contents

Summary

Procaryotic microorganisms (*Bacteria* and *Archaea*) generally appear as small rods or cocci of a few micrometers at most in size. At first sight they possess few distinguishing structural features, especially when compared with the highly diverse world of the eucaryotic microorganisms. However, upon more thorough examination it becomes clear that the procaryote world contains a surprising diversity of morphological variability, enabling an optimal adaptation to environmental conditions, dispersal of the

species, and if necessary, survival when conditions become unfavorable for growth.

Some procaryotes increase their surface-to-volume ratio by producing diversely shaped appendages (prosthecae), and even thin, flat square organisms exist in the domain *Archaea*. Some procaryotes may be extremely large: several types of *Bacteria* as big as 0.3-0.5 mm have recently been recognized. Procaryotic cells may form specialized extracellular structures such as fimbriae and pili, and extracellular polysaccharide layers commonly occur. A variety of intracellular structural components may be found, such as intracellular membranes to increase membrane surface, as well as different types of storage materials. To position themselves where life conditions are optimal, many procaryotes possess motility organelles such as flagella, intracellular magnetite particles (magnetosomes) may aid some species in their orientation, and gas vesicles may confer buoyancy.

A variety of survival and dispersal forms also exists, some of them being extremely resistant to adverse conditions. Finally, some colonial procaryotes display a considerable degree of multicellular differentiation, sometimes involving complex life cycles in which cells of different morphological and physiological properties alternate.

1. Introduction

The variety of life forms on Earth is bewildering, and the diversity of form, function and adaptation is tremendous. This is even true for the simplest microbial life forms inhabiting our planet. Eventually all this diversity and these adaptation mechanisms have one common goal: to optimize life conditions and to aid the organisms in survival and reproduction. As François Jacob wrote in 1973: "A bacterium, an amoeba … what destiny can they dream of other than forming two bacteria, two amoebae …?"

This article will discuss the morphological diversity in microorganisms with special emphasis on the procaryote world. The procaryotes (domains *Bacteria* and *Archaea*) represent two out of the three domains in which living organisms are classified (see *Systematics of Archaea and Bacteria*). The metabolic diversity within these groups is extremely varied (see *Metabolic Diversity in Procaryotes and Eucaryotes*), and greatly exceeds the metabolic diversity shown by the eucaryotes. Morphologically the procaryotes may seem little exciting at first sight, even when their ultrastructure is examined with the electron microscope. However, upon a more thorough examination, we may recognize a surprising variety of morphological and behavioral adaptations as a reaction to environmental stimuli. This article attempts to provide an overview of the morphological diversity in procaryotic microorganisms and explore the functional aspects of this diversity. Finally, a short presentation of the functional morphological aspects of eucaryotic microorganisms will be given as well.

2. Cell Size and Cell Shape in the Procaryotes

Most species of procaryotic microorganisms, *Bacteria* as well as *Archaea*, appear as small rods or cocci of a few micrometers in size at most, and the majority of species have few morphologically distinguishing features, especially when compared with the highly diverse world of the eucaryotic microorganisms (see *Protoctista: Systematics of*

"Lower Eucaryotes" and *Diversity of Form, Function and Adaptation in Fungi*). However, the diversity in size and shape is much greater than generally assumed. Procaryotic cells as small as 0.5 μm and as large as 0.3-0.5 mm are known, and some species display truly unusual shapes.

2.1. Small is Powerful

For organisms that multiply rapidly (doubling times of half an hour and shorter are not uncommon in the procaryote world), a small cell size is advantageous as the rate at which nutrients may enter the cell and waste products can be excreted primarily depends on the surface area of the cytoplasmic membrane. For a spherical cell with a radius r, the cell volume is $^4/_3\pi r^3$, the surface area equals $4\pi r^2$, and the surface to volume ratio can thus be expressed as 3/r. Thus, the smaller the cell, the larger the surface-to-volume ratio.

Small cells are especially abundant in low nutrient environments. Microscopic examination of the planktonic bacterial community in the oligotrophic ocean reveals that most of cells are smaller than 1 μm, often even smaller than 0.5 μm. In some cases it has been proven that the smallness of the cells is an inherent property of the species. In other cases, cell size may depend on the nutritional status: nutrient-starved cells are often much smaller than cells growing in the rich medium in which all required nutrients are present in excess. Attempts to isolate bacteria adapted to life at low nutrient concentrations often yield spirally-shaped cells, increasing the surface-to-volume ratio not by size reduction but by their specialized cell morphology.

2.2. Appendages and Other Strategies to Increase Cell Surface

Another strategy to increase the surface-to-volume ratio and thus to increase the area of the cell membrane and enhancing the potential of nutrient uptake is the formation of prosthecae, appendages consisting of extrusions of cytoplasm, bounded by the cell wall. Prosthecate bacteria often have exotic shapes. Such prosthecate bacteria are especially abundant in oligotrophic water bodies, and can often be found attached to surfaces. Other well-known examples of prosthecate bacteria adapted to life at low nutrient concentrations are *Hyphomicrobium* and *Caulobacter*. These intriguing microorganisms have complex life cycles, and these will be discussed in more depth in section 7.3.

One of the most exotic shapes found in the procaryote world is the perfectly square, thin, flat shape of certain *Archaea* that occur in brine pools and in saltern crystallizer ponds at salt concentrations at or approaching saturation. These square procaryotes were first described in 1980. They were recognized as bacteria on account of the gas vesicles they contain (see also section 5.3). Such square *Archaea* may have a length of 3-5 μm, but they are no more than 0.2 μm thick. Figure 1 illustrates these unusual microorganisms. The square halophilic *Archaea* have recently been brought into culture, their genome has been sequenced, and we have learned much about their physiology. It may be assumed that the large surface-to-volume ratio aids the cells in obtaining nutrients and/or oxygen (the solubility of oxygen is greatly decreased in salt-saturated brines). Realizing that most living cells maintain a turgor pressure that pushes the cytoplasmic membrane to the cell wall, one may ask how a flat, square morphology is feasible at all for a living cell, as such a shape is not expected to withstand even low pressures from within. The answer lies in the observation that halophilic *Archaea* lack a measurable turgor pressure. This does not provide an explanation for the question why cells may be square, but it does explain why this flat square type of cell can occur in Nature at all.

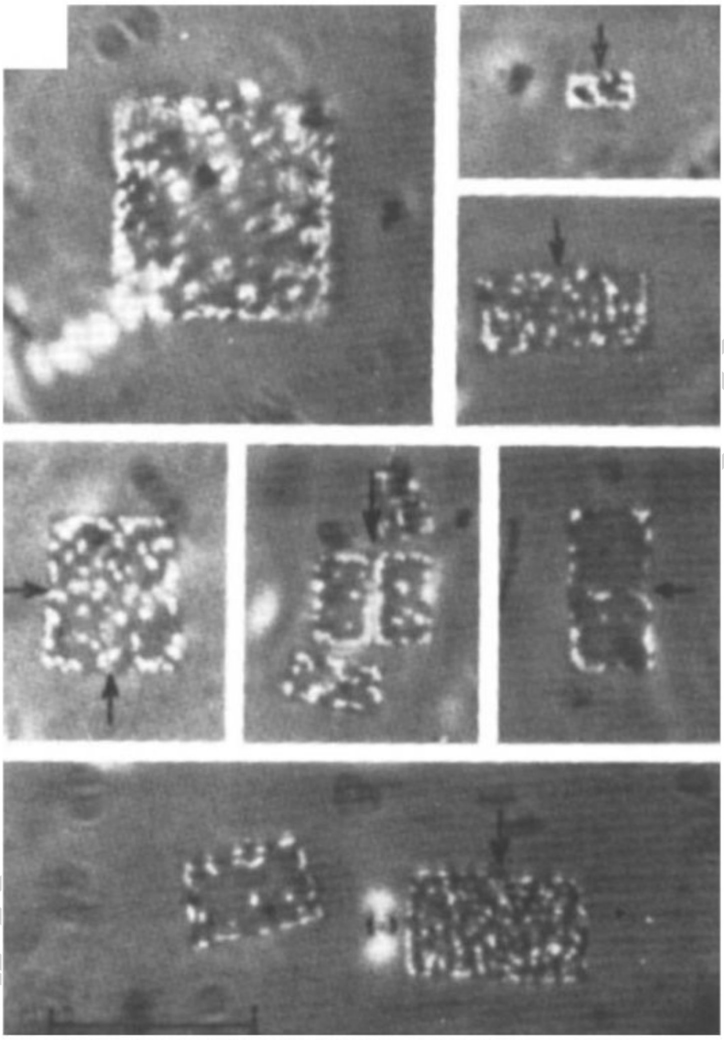

Figure 1. Phase contrast micrographs of square *Archaea* from a brine pool at the coast of the Sinai peninsula, Egypt. The light areas are gas vesicles. Scale bar, 10 μm. From Walsby A.E. (1980), Nature 283: 69-71; Reproduced with permission.

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Bibliography

Angert E.R., Clements K.D. and Pace N.R. (1993). The Largest Bacterium. *Nature* **362**, 239-241. [The description of "Epulopiscium fischelsoni" found in the intestine of a surgeonfish, being the largest known prokaryotic cell, until the discovery in 1999 of *Thiomargarita namibiensis*].

Beveridge T.J. (1989). *The Structure of Bacteria*. pp. 1-65 in: Poindexter J.S. and Leadbetter E.R. (Eds.), *Bacteria in Nature. Vol. 3. Structure, Physiology, and Genetic Adaptability*. New York: Plenum Press. [A beautifully illustrated treatise on the ultrastructure of procaryotes, including discussions on special structures such as gas vesicles, magnetosomes, intracellular membrane systems, etc.]..), Vol. 3, pp. 113-164. Springer, New York.

Dworkin M., Falkow S, Rosenberg E, Schleifer K.-H. and Stackebrandt E. (Eds.) (2006). *The Prokaryotes. A handbook on the Biology of Bacteria: Ecophysiology and Biochemistry*. 3rd ed., New York: Springer-Verlag. [The new edition of the leading handbook on all groups of procaryotes, published in 7 volumes, each chapter having been written by specialists on each group; Chapters of special interest relating to the subject of this chapter are the chapters by Dworkin M., *Prokaryotic Life Cycles*, Vol. 2, 102-139, by Poindexter J.S., *Dimorphic Prosthecate Bacteria: The Genera* Caulobacterium, Asticcacaulis, Hyphomicrobium, Pedomicrobium, Hyphomonas, *and* Thiodendron, Vol. 5, 72-90,, by Jurkevitch, E., *The Genus Bdellovibrio*, Vol. 7, 12-30, and by Spring S. and Bazylinski D.A., *Magnetotactic Bacteria*, Vol. 2, 842-862].

Lengeler J.W., Drews G. and Schlegel H.G. (1999). *Biology of the Prokaryotes.* Stuttgart: Thieme. [A comprehensive textbook on the biology of procaryotes; Chapter 2: *Cellular and Subcellular Organization of Procaryotes* (pp. 20-46) gives an excellent overview of the procaryote ultrastructure and the morphological attributes of special organelles].

Madigan M.T., Martinko J.M., Dunlap, P.V., and Clark, D.P. (2009). *Brock Biology of Microorganisms.* 12th ed. San Francisco: Pearson/Benjamin Cummings. [A comprehensive, beautifully illustrated basic textbook, presenting excellent overviews of the taxonomy of procaryotes and the properties of the different groups].

Schulz H.N., Brinkhoff T., Ferdelman T.G., Hernández Mariné M., Teske A. and Jørgensen B.B. (1999). Dense Populations of a Giant Sulfur Bacterium in Namibian Shelf Sediments. *Science* **284**, 493-495. [The description of *Thiomargarita namibiensis*, the largest procaryote known thus far].

Walsby A.E. (1980). A Square Bacterium. Nature **283**, 69-71. [The original description of the presence of flat, gas-vacuolate square *Archaea* in hypersaline environments].

Walsby A.E. (1994). Gas Vesicles. *Microbiol. Rev*. **58**, 94-144. [An authoritative review of all aspects of gas vesicles in procaryotes, including in-depth discussions of their morphology, genetics, regulation of their formation, and ecological function].

Biographical Sketch

Prof. Aharon Oren was born in 1952 in Zwolle, the Netherlands. He obtained his M.Sc. degree (microbiology and biochemistry) (1974) from the University of Groningen and his Ph.D. degree in microbiology (1978) from the Hebrew University of Jerusalem. He has been on the staff of the Hebrew University as research fellow (1979-1982), lecturer (1984-1985), senior lecturer (1985-1991), associate professor (1991-1996) and professor of microbial ecology (since 1996). He has been post-doctoral fellow (1982-1983) and visiting assistant professor (1983-1984) at the University of Illinois at Urbana-Champaign. Functions performed by Prof. Oren include: member (since 1989) and secretary (since 1994) of the International Committee on Systematics of Prokaryotes subcommittee on taxonomy of Halobacteriaceae, member of the International Committee on Systematics of Prokaryotes subcommittee on the taxonomy of photosynthetic prokaryotes (since 1991), member of the editorial board of the International Journal of Salt Lake Research (1991-1999), editor of FEMS Microbiology Letters (1994-present), director of the Moshe Shilo Minerva Center for Marine Biogeochemistry (1995-2000), head of the Division of Microbial and Molecular Ecology, The Institute of Life Sciences at the Hebrew University of Jerusalem (1998-2003), co-opted member (1999-2002), chairman (2002-2008), and executive secretary/treasurer of the International Committee on Systematics of Prokaryotes (2008-present), member of the Executive Committee (1999-2002) and vice-president (2002-present) of the International Society for Salt Lake Research affiliate professor of George Mason University, Fairfax, Virginia (1999-present), associate member of Bergey's Manual Trust (2001-present), member of the editorial board of Extremophiles (2001-present), associate editor of the International Journal of Systematic and Evolutionary Microbiology (2001-present), member of the Editorial Review Board of Archaea (2004-present), and associate editor of Saline Systems (2005 – present). Prof. Oren was the recipient of the Moshe Shilo prize of the Israel Society for Microbiology for 1993 and of the Ulitzki prize of the Israel Society for Microbiology for 2004, and was elected fellow of the American Academy of Microbiology in 2000. Prof. Oren has published nine books and over three hundred research articles, reviews, and book chapters.