Microbiol Monogr (2)
J.M. Shively: Complex Intracellular Structures in Prokaryotes
DOI 10.1007/7171_018/Published online: 13 May 2006

Prokaryote Complex Intracellular Structures: Descriptions and Discoveries

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Abstract The gas vacuole was first observed in 1895, but details of this structure (gas vesicles) as well as discovery of the other structures covered in this monograph (proteasomes, phycobilisomes, chlorosomes, carboxysomes and carboxysome-like inclusions, magnetosomes, intracytoplasmic membranes, membrane-bounded nucleoids, pirellulosomes, anammoxosomes and the cytoarchitecture of *Epulopiscium* spp.) awaited the availability of the transmission electron microscope and related technologies. Additional advancements in electron microscopy were required for the optimal visualization of some structures.

1 Introduction

It is quite interesting to peruse microbiology textbooks from the 1950s (for example Stanier et al. 1957). As a rule and although several different cell inclusions are briefly discussed, including glycogen, granulose, fat, volutin, and sulfur (see Vol. 1 of this series), little information is presented on any complex intracellular structures. DNA was known, but the presence/absence of a nucleus and mitotic figures in bacteria was still a controversial subject. The molecular mechanisms of protein synthesis are missing, including information on ribosomes. Chromatophores, recently isolated but not yet

observed in the cell, containing the photosynthetic pigments are briefly described as "special structures" (see chapter by Niederman, this volume). Surprisingly, gas vacuoles discovered in cyanobacteria in 1895 and in bacteria in 1913 (Fig. 1) are not even mentioned (see chapter by Pfeifer, this volume). In defense of the omission, definitive work on the vacuoles did not occur until 1956 and later. Also, cyanobacteria, still considered to be

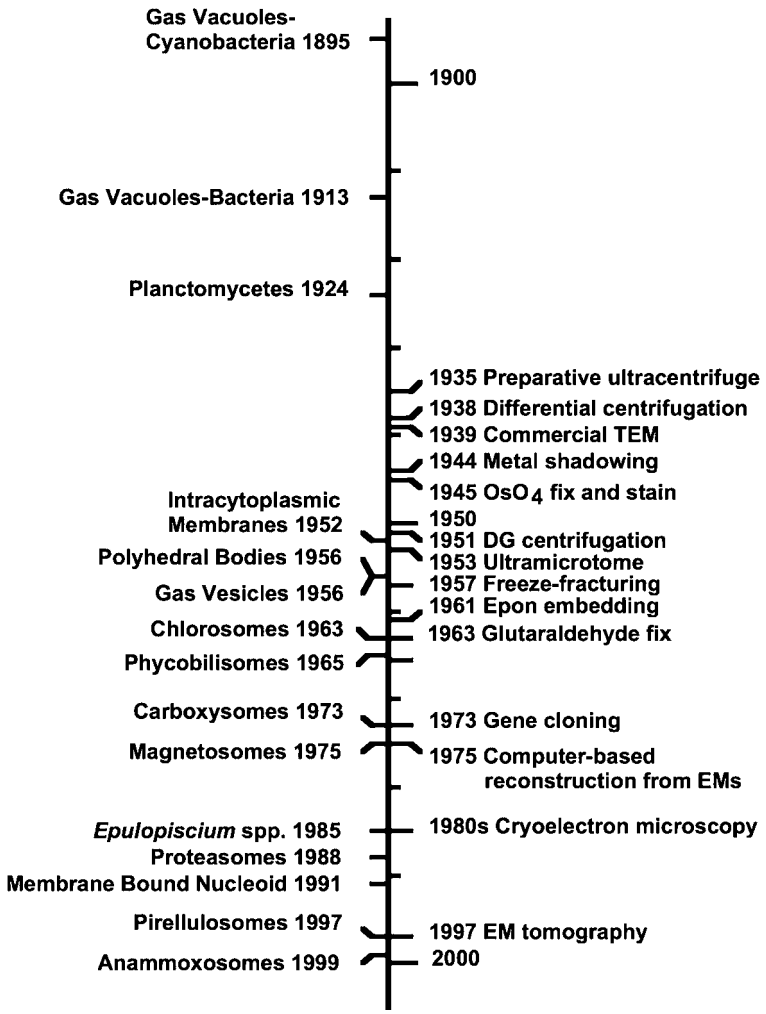

Fig. 1 Timeline of complex intracellular structure discovery (*left*) and selected technological advances (*right*). Abbreviations: *TEM* transmission electron microscope, *DG centrifugation* density gradient centrifugation, *SEM* scanning electron microscope, *EMs* electron micrographs, *EM tomography* electron microscope tomography. Technological advance dates taken from Alberts et al. (2002) and Beck (2002)

the "property" of plant scientists, were yet to become a part of the realm of microbiology. However, even botany textbooks provided poor coverage of the cyanobacteria; they were generally only well covered in separate monographs. Essentially, the only complex structure given much attention was the endospore found in certain bacteria. Thus, the "primary" complex intracellular structure topics (proteasomes, phycobilisomes, chlorosomes, gas vesicles, carboxysomes and carboxysome-like inclusions, magnetosomes, intracytoplasmic membranes, the membrane-bounded nucleoids and pirellulosomes, anammoxosomes, and cytoarchitecture of *Epulopiscium* spp.), presented as chapters in this volume, were unknown except for the preliminary information on gas vacuoles and chromatophores. This lack of information on the now-known complex intracellular structures was essentially due to "what you can't or don't see (resolve), you can't describe".

The gas vacuole is actually composed of gas vesicles and the chromatophore is a part of an extensive intracytoplasmic membrane system; neither of these structures can be resolved in the light microscope. The same is true for many of the other structures, and in some instances the structures are so uncommon that their serendipitous discovery was required even if they could have been resolved. Therefore, the discovery of complex intracellular structures necessitated the introduction of a new technology, namely the electron microscope and related technologies, as well as the careful ultrastructural characterization of known and newly isolated prokaryotes (Fig. 1). Admittedly, other technologies, encompassing many disciplines, are also of paramount importance and are required to fully understand a structure; this remains true today. The discovery and characterization of complex intracellular structures in prokaryotes continues into this century.

A brief description and the historical background of each "primary" intracytoplasmic structure mentioned above will be presented in this introductory chapter. Subsequent chapters (this volume) by Maupin-Furlow et al., Adir et al., Frigaard and Bryant, Pfeifer, Heinhorst et al., Scheffel and Schüler, Niederman, Fuerst, Fuerst et al., and Angert provide in-depth coverage of each structure.

After the "primary topics" for this volume were selected, colleagues and authors suggested several other interesting structures. In an effort to provide more complete coverage, but still remain within the established guidelines for the length of the monograph, seven structure topics were added as mini (cameo) chapters: see chapters authored by Vollmer, Kürner et al., Balish, Hoiczyk, Sergueev et al., van Keulen, and Corsaro and Venditti in this volume.

2
Complex Intracellular Structures: Descriptions and Discovery

The structures vary from those that exist as either naked protein or protein–lipid (membrane) complexes to those that are enclosed in either a monolayer protein coat or bilayer membrane(s), to those that represent intracellular "active" offspring.

2.1
Proteasomes

Proteasomes, intracellular nanocompartments, are energy-dependent proteases that degrade proteins into 3–30 amino acid oligopeptides (Baumeister et al. 1998; Bochtler et al. 1999; De Mot et al. 1999; Maupin-Furlow et al. 2000, 2001; Zwickl et al. 2000). The structures are ubiquitous in both eukaryotes and archaea but are rare in bacteria, having been identified only in actinomycetales. The 20S catalytic core, 11–12 nm in diameter by 15 nm in length, is a cylinder (four-stacked heptameric rings) with narrow openings at each end allowing limited substrate access to the central chamber where hydrolysis takes place (Zwickl et al. 2000; Maupin-Furlow et al. 2000, 2001; Kaczowka and Maupin-Furlow 2003). In both eukaryotes and archaea the 20S core associates with ATPase regulatory components, 19S cap and proteasome-activating nucleotidase (PAN), respectively, to form the energy-dependent complex (Zwickl et al. 1999; Maupin-Furlow et al. 2001; Kaczowka and Maupin-Furlow 2003). The bacterial 20S proteasome is thought to associate with ARC (ATPase forming ring-shaped complexes), but the ability of ARC to facilitate protein unfolding and/or the association with 20S proteasomes remains to be established (Wolf et al. 1998).

Although proteasome-like structures were first described in eukaryotes in the early 1960s (Baumeister et al. 1997, 1998), it was not until 1988 that enzymological studies revealed an array of proteolytic activities that lead to a consensus name "multicatalytic proteinase" (Dahlmann et al. 1988). However, that same year Arrigo et al. (1988), recognizing the structure as a functional compartment, suggested the name "proteasome". Dahlmann et al. (1989, 1992), noting that archaea possess some properties reminiscent of eukaryotes, investigated the archaebacterium, *Thermoplasma acidophilum*, and discovered the presence of proteolytically active particles (prosome/proteasome) similar in shape to those of eukaryotes. Although it was suggested that proteasomes were restricted in the Archaea to *Thermoplasma* (Pühler et al. 1994), Maupin-Furlow and Ferry (1995) demonstrated their presence in a methanogenic archaeon, *Methanosarcina thermophila*. Genome sequences now reveal that they are ubiquitous in the Archaea. The first bacterial 20S proteasome was found in the actinomycete, *Rhodococcus erythropolis*

(Tamura et al. 1995; Zuhl et al. 1997). A chapter by Maupin-Furlow et al., this volume, provides in-depth coverage of proteasomes.

2.2 Phycobilisomes

Phycobilisomes are supramolecular protein complexes present in both prokaryotic (cyanobacteria) and eukaryotic cells (cyanelles, red algae) (Shively 1974; Gantt 1980; Glazer 1985; Shively et al. 1988; Sidler 1994; Tandeau de Marsac 2003; Adir 2005). The phycobilisomes, attached to photosynthetic lamellae and functioning as the light-harvesting antennae for photosystem II, are primarily composed of intensely pigmented phycobiliproteins, and smaller amounts of non-chromophore bearing "linker peptides". There are three major phycobiliprotein families: phycocyanins, allophycocyanins, and phycoerythrins present in red algae and cyanobacteria (Sidler 1994; Tandeau de Marsac 2003). Electron microscopy reveals the morphology of the phycobilisome to be quite variable depending on the organism, with four different types having been described: hemi-ellipsoidal, hemi-discoidal, block shaped, and bundle shaped (Shively et al. 1988; Sidler 1994; Tandeau de Marsac 2003; Adir 2005).

Esenbeck (1836) reported on a water-soluble blue-colored pigment he labeled "saprocyanin" (later named phycocyanin) that was released from the cyanobacterium *Oscillatoria*. During the rest of the 19th century and well into the 20th century additional phycobiliproteins were discovered and their various properties described (Sidler 1994; Tandeau de Marsac 2003). Myers and Kratz (1955) and Myers et al. (1956) determined that phycobiliproteins were major constituents of cyanobacteria and red algae and theorized that the 22 nm granules observed between the thylakoids were actually phycobiliprotein aggregates. In an elegant series of studies on the ultrastructure of the red alga *Porphyridium cruentum*, Gantt and Conti (1965, 1966a,b) demonstrated that phycobiliproteins were present as 40 nm granules arranged in regular rows on the stromal surfaces of the thylakoids. They named the granules phycobilisomes. Lefort (1965) observed the structures in the cyanobacterial endosymbionts, but did not identify the structures as phycobilisomes until later (Bourdu and Lefort 1967). Gantt and collaborators as well as other research groups reported on the presence of phycobiliproteins in diverse red algae and cyanobacteria (Edwards et al. 1968; Gantt and Conti 1969; Edwards and Gantt 1971; Gantt 1980). Gantt and Lipschultz (1972) developed a method for the isolation of the structures from *P. cruentum* and later the method was modified for the isolation of phycobilisomes from cyanobacteria (Gray et al. 1973), thus paving the way for extensive studies of the phycobilisomes. The relative ease of isolation and purification of various phycobilisome components enabled researchers to perform very detailed spectroscopic and crystallographic studies, which afforded a precise molecular view of the structure and func-

http://www.springer.com/978-3-540-32524-6

Complex Intracellular Structures in Prokaryotes
Shively, J.M. (Ed.)
2006, VIII, 379 p. 85 illus., 23 illus. in color., Hardcover
ISBN: 978-3-540-32524-6