

Preface

The planctomycetes have been from the moment of their discovery organisms on the edge of our understanding, on the frontier of our knowledge of what microorganisms might be like, forming new models for microbial life and for biology. They have from this time on posed many fascinating and stimulating problems regarding their true identity, their evolutionary relationships, and their cell structure and biology. Even their name reflects this intriguing ambiguity—encapsulating the idea as actinomycetes once did that a eukaryote affinity might exist. The basis for that early decision—morphological similarity with fungi—is now not supportable since the pioneer work of Jean Schmidt and Mortimer Starr revealed the non-cellular nature of the stalks mistaken for mycelia in those early aquatic rosettes of *Planctomyces bekefi* seen originally only via light microscopy (Chapter 1). Perhaps though the time is not yet ripe to unreservedly apply the name ‘planctobacteria’ to these organisms as some have done informally. Planctomycetes have since Gimesi’s time emerged as organisms with an internal organizational plan which appears to be one of the most complex known in bacteria or archaea—the cell contents are divided by internal membranes into two or even three distinct compartments, the nucleoid DNA is tightly folded, and in some cases membrane vesicles can form, imparting the ability to incorporate macromolecules from the environment analogous to eukaryote endocytosis and probably via similar molecular mechanisms (Chapters 2 and 3). They are indeed new models for cell structure, stretching our imagination of what a bacterial cell can look like and challenging our concept of a ‘prokaryote’ at the purely organizational level (without even considering the impact of phylogenetics and Archaea on this concept). The pure culture models for planctomycete cell biology and genetics *Gemmata obscuriglobus*, *Planctomyces limnophilus* and *Rhodopirellula baltica* have been central to our progress in these areas. Planctomycetes are of central significance to evolutionary microbiology and cell biology and must be taken into account in any future theories of eukaryote and eukaryote nucleus origins (Chapter 11). Thus, planctomycetes are of wide significance not only to microbiology but also to the biology of most organisms visible to the naked eye and must be taken into account if we are to solve major problems of biology concerning the marked transitions in life’s evolution involving cellular

complexity. Changing perspective to our contemporary global problems, planctomycetes are also ready to help. There are now immense bioreactors at industrial scale, from the Netherlands city of Rotterdam to a monosodium glutamate factory in China, where anaerobic ammonium-oxidizing planctomycetes (Chapter 4) help us clean up environmental ammonia-rich waste while saving energy and reducing our CO₂ footprint. In addition, marine versions of these planctomycetes are central to the global nitrogen cycle, responsible for at least 50 % of nitrogen removal from marine ecosystems, and substantial amounts of the nitrogen we breathe may be produced by marine anammox species growing in oxygen-minimum zones of the world's oceans; regions thought to inevitably increase with increasing global warming. This anammox process is dependent on the internal membrane-bounded compartment known simply as the anammoxosome, a body which may be a true energy-generating organelle, one unique within the bacteria, but bearing comparison with eukaryotic mitochondria in some ways (Chapter 4). New unusual habitats such as acid peat bogs have excitingly revealed new taxonomic diversity among the planctomycetes and thrown light on the potential breadth of their ecological roles and importance (e.g. in microbial communities of ecosystems under threat with global climate change) (Chapter 5). If this were not enough microbiological stimulation from one bacterial group, it turns out that they harbour enzymes known previously from C1 transfer pathways involving methane generation and oxidation, and which may be significant for our understanding of how such major geomicrobiological processes for the global carbon cycle may have originated (Chapter 8). Of course, the answers to many of our questions regarding planctomycete cell biology and biochemistry may await the development of genetic systems so powerful for analysing the functions of genes in other bacteria—promising progress is being made to give planctomycetologists these essential molecular tools, and proteomics has already made progress in the understanding of unique features such as the protein cell wall of the model marine planctomycete *Rhodopirellula baltica* (Chapter 6). In the meantime, genomics and bioinformatics are revealing important features for our understanding and will provide a solid necessary basis for any future experimental genetics (Chapter 7). One of the remarkable features of planctomycetes revealed by genomics complemented is their possession of enzymes for pathways manipulating C1 compounds (Chapter 8), but in the apparent absence of methane oxidizing or generating abilities. Whatever their contemporary function, these enzymes are of great evolutionary interest, since they seem to be quite divergent from those known in other bacteria and in archaea, and perhaps go back to the very beginnings of methane biogeochemistry on Earth.

Beyond planctomycetes, we now know that planctomycetes have relatives within the bacteria, in the PVC superphylum, and comparative cell biology and genomics between members of this superphylum may form one of the keys to understanding their evolution. New extremophile PVC verrucomicrobia in the genus *Methyloacidiphilum* (Chapter 9) which, in contrast with planctomycetes, possess both C1 transfer pathways and methane oxidation metabolism, have added to our understanding of the immense physiological diversity within the PVC superphylum, encompassing as it does not only this thermoacidophilic methane oxidizer but also mesophilic aerobic chemoheterotrophs such as *Gemmata obscuriglobus*, the

moderately thermophilic phototactic planctomycete *Isosphaera pallida*, obligately anaerobic chemolithoautotrophs like the anammox planctomycetes, anaerobic human intestinal microbiome organisms like *Akkermansia muciniphila* in the verucomicrobia and *Victivallis vadensis* in the Lentisphaerae, as well as the obligate intracellular pathogens in the phylum *Chlamydiae* (Chapter 10). Of necessity, this book discusses only some of the many significant PVC species beyond the planctomycetes.

Perhaps one of the reasons that planctomycetes and their relatives are frontier microorganisms is that they indeed include some very ancient bacteria representing some features of the pioneer habitats first available on the early earth (in the case of the anaerobic anammox ‘ammonium eaters’) and perhaps some features of the very earliest eukaryotes or even a eukaryote-like last common ancestor of the 3 Domains (Chapter 11). Analyses of the likely nitrogen cycle on the early Earth, for example, suggest that anammox planctomycetes were the first producers of nitrate on the planet and that anammox was the only process which could have closed the nitrogen cycle returning fixed nitrogen to the dinitrogen pool in the anaerobic biosphere. If alternatively planctomycetes or their ancestors did later on contribute by gene transfer or more direct vertical inheritance to the molecular basis of eukaryality, those events must have been ancient also. The phylogenetic and bioinformatic analyses are still controversial on how ancient planctomycetes and their closest relatives may be and on how homologous their eukaryote-like features to eukaryotes might be. Whatever the case, due to their widespread presence and activities they are one of the central microbial keys to understanding natural aquatic, terrestrial and perhaps even human microbiome microbial communities, and are a key to understanding the possible mechanisms of origin of the type of cell organization our very own human cells have inherited from the first eukaryote. They may thus form a model for origins of the biology of the modern cell and a key to truly understanding our own biology at the deep evolutionary level. As the late Carl Woese, the great discoverer of the Archaea and the three Domains of life emphasized, without such an evolutionary understanding there is no truly deep understanding of any life, that essentially historical entity.

Planctomycetes and their relatives are an excellent example of how understanding the true extent of microbial diversity can yield insights for science unimaginable if our focus was trained exclusively on *E. coli*. I would like this book also to widen your microbial, biological and scientific horizons to include the planctomycetes, new models for cell structure, origins and biology.

I would like to express my sincere thanks to all our authors—their great contributions have made this first book on planctomycetes focused on their cell biology possible. We would hope that in the future there will be another volume wholly devoted to the significant ecology and environmental significance of the planctomycetes. I also extend my thanks to Springer for publishing this book, one which will be immensely valuable for those in the field of planctomycetology and those entering it for the first time (of whom we hope there will be many more!).



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