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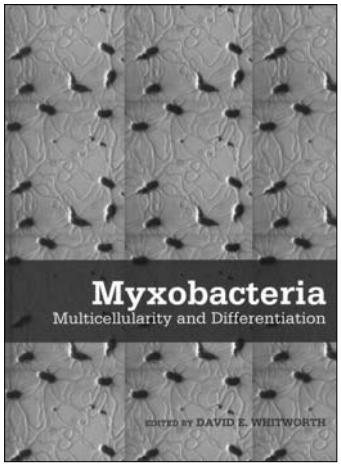

Myxobacteria: multicellularity and differentiation

DAVID E. WHITWORTH (ED)

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Myxobacteria—a group of gram-negative soil bacteria belonging to the class Deltaproteobacteria—have long fascinated microbiologists for several reasons. They possess the largest genomes described for prokaryotes and are able to glide over solid surfaces even though they lack flagella. Moreover, the complex patterns of behavior displayed by myxobacteria are more typical of those of eukaryotes. For example, myxobacteria engage in multicellular cooperative hunting and feeding and have been called wolf packs, as they consume all the microbial cells they encounter by secreting antibiotics and enzymes that kill and lyse cells, after which they consume the products of this process. Myxobacteria also produce spore-forming fruiting-body aggregates. When food is scarce, cells on a solid surface initiate a complex cellular response in which thousands of cells aggregate to form a fruiting body, part of which later differentiates into environmentally resistant spherical myxospores. This behavior, together with the possibility of distinguishing myxobacterial species on the basis of fruiting-body shape, color and size, implies a highly coordinated system of signaling between individual cells. Since their growth and development are marked by cell-to-cell interactions, myxobacteria have been referred to as "social," and the nature of these interactions has been the focus of recent myxobacterial research.

Myxobacteria: multicellularity and differentiation is a detailed collection of 30 multi-authored papers that discuss such topics as the mechanisms of myxobacterial motility, cellular differentiation, cellular regulation, genetics, metabolism, and metabolite production in a volume comprised of eight different sections. The two introductory chapters of Section I (Myxobacterial Biology), address the historical, ecological, and evolutionary contexts of myxobacterial research. This reveals that *Myxococcus xanthus* is the best-studied myxobacterium, providing a model for the previously described multicellular mechanisms. In Section II (Development and Motility), Chapter 3 deals with early developmental events and then goes on to discuss how individual *M. xanthus* cells are able to perceive a decrease in nutrient availability, recognize individual and population starvation, and then integrate this information to initiate fruiting-body formation and cellular differentiation.

The signaling molecules involved in quorum-sensing by myxobacteria are neither acylated homoserine lactones nor autoinducer-2 molecules; instead, these bacteria make use of an A-signal and a C-signal. The latter is a cell-surface-associated protein that has been shown to play a central role in fruiting-body morphogenesis in *M. xanthus*. Chapter 4 reviews our current understanding of how the C-signal acts at a molecular level to induce and coordinate events that are separate in space and time.

Motility is a significant physiological adaptation that facilitates the growth and survival of many species of bacteria in their natural habitats. Of these, *M. xanthus* display what has been termed gliding motility. In *M. xanthus*, gliding motility involves two independent gene systems controlling two types of gliding, one adventurous and one social . Chapters 5 and 6 examine the detailed mechanisms of action of these molecular motors, as well as the components important for engine reversal. It is hypothesized that regulated cell reversals are required for *M. xanthus* to undergo directed motility. Thus, Chapter 7 presents the Frz chemosensory system, the mechanism controlling the frequency at which cells reverse their direction of movement.

Section III discusses regulatory mechanisms. Here, Chapter 8 reviews the eight chemosensory signal transduction systems found in *M. xanthus*, while Chapter 9 focuses on the transcriptional regulatory mechanisms essential to *M. xanthus* development. While the *cis*-acting DNA elements and *trans*-acting proteins interacting with particular sigma factors have been identified for several developmental genes, much remains to be discovered concerning regulatory strategies and their mechanisms.

Myxobacteria live in an ever-changing environment and therefore rely on signal transduction to couple the perception of environmental changes (physical, chemical, and biological stimuli) with suitable behavioral responses. This is accomplished through the regulation of specific subsets of genes or operons. Signaling pathways can take different forms but are grouped into families according to their shared features. In prokaryotes, the largest family of signaling pathways is the two-component system (TCS), which is able to adapt to a range of physiological processes. Exceptionally abundant in myxobacteria, TCSs are described in Chapter 10. Ser/Thr/Tyr kinases and protein phosphatases that function as biological "on" (phosphorylation) and "off" (dephosphorylation) switches of the signal transduction pathways regulating gene expression during *M. xanthus* development are the subject of Chapter 11.

Myxobacteria frequently appear as brightly colored colonies and sporiangioles, due to their expression of carotenoids and other pigments, the main role of which is to protect cells against photo-oxidative damage. However, these pigments are also involved in light harvesting, where they function as redox intermediates in the shuttling of electrons during photosynthesis and as precursors for the molecules required in photoreception and hormonal action. Chapter 12 provides an update on our understanding of the many aspects of the complex regulatory network of carotenogenesis in *M. xanthus*, one of the most important model systems for the genetic analysis of this process.

A microorganism's cell wall is a key component in cell-cell interactions and thus in cellular signaling pathways. The importance of the cell wall structure is examined in Section IV (Structure and Metabolism). Chapter 13 covers in detail the polysaccharide-containing components of the *M. xanthus* cell envelope, including peptidoglycan, lipopolysaccharide, extracellular matrix, and exopolysaccharide. Chapter 14 discusses the catabolism of amino acids and lipids, the main energy sources myxobacteria use when lysing their prey. Particular emphasis is placed on the anabolism of lipids, given the unusual chemical structures of these molecules in myxobacteria, as well as on the synthesis of two spore-specific products, trehalose and ether lipids. Chapter 15 reviews recent developments that have allowed the enormous chemical diversity found in myxobacteria to be exploited. It is now well-appreciated that myxobacteria, together with ascomycetes and fungi, are the sources of many significant microbial natural products, including secondary metabolites not found in other sources.

The sequencing of the myxobacterial genome was released in 2001 and later complemented by additional random sequencing published in 2006. The resulting information forms the background of Section V (Myxobacterial Genomics and Postgenomics). Chapter 16 discusses and compares the genomic sequences of *M. xanthus* and *Stigmatella aurantiaca*, two related aerobic, fruiting-body–forming myxobacteria, while Chapter 17 provides a postgenomic overview of *M. xanthus*, highlighting some of the genomic-scale biological research and the use of functional genomics to predict novel cellular and chemical interactions. New techniques being developed will allow us to continue to discover and understand the great network of genes that form the basis of *M. xanthus*' fascinating lifestyle.

Two chapters of Section VI are devoted to two species of myxobacteria: *S. aurantiaca* and *Sorangium cellulosum*. The structure and complexity of the fruiting bodies as well as the production of the signaling pheromone stigmolone are the primary characteristics that distinguish *S. aurantiaca* from *M. xanthus*. *S. cellulosum*, a cellulose-degrading myxobacteria, is the most potent producer of secondary metabolites in its group and has the largest bacterial genome sequenced to date.

In Section VII (Analogous Systems), seven chapters (Chapters 20–26) are devoted to analogous systems found in other microorganisms, thereby setting myxobacterial biology in a much broader context. For example, *Bdellovibrio* species of Deltaproteobacteria can be isolated from soil environments similar to those in which myxobacteria are found. Although *Bdellovibrio* species share many features with myxobacteria, such as the use of hydrolytic enzymes to kill and digest other bacteria, these flagellate and fast-swimming organisms present significant genomic differences. Another species that exhibits multicellular behaviors is *Bacillus subtilis*, whose biofilm formation and swarming motility resemble the fruiting-body development and social motility of *M. xanthus*. In both microorganisms development is environmentally signaled. In contrast, in stalked Alphaproteobacteria such as *Caulobacter crescentus*, development does not depend on environmental conditions but is part of normal progression through a cell cycle in which swarmer daughter cells produced in every cycle represent an alternative strategy for coping with the almost constant condition of famine that is characteristic of this microorganism's environment. Myxobacteria also have a number of traits in common with the eukaryotic *Dictyostelium discoideum*. Upon starvation, both aggregate to form a multicellular structure, the spore-containing fruiting-body. Both organisms have evolved the same basic response to nutrient deprivation, but the methods by which those responses are elicited are unique. A comparison of their biochemical pathways will lend insight into how different organisms can use a wide range of mechanisms to achieve the same goals.

The book's final section (Chapters 27–30), is a collection of useful methods for the cultivation, manipulation, and characterization of myxobacteria, including specific protocols for analyzing their motility, development, and gene expression. There is also a section on the genetic tools available to expand beyond single-gene studies to an evaluation of the relationships between multiple genes in a genetic pathway as well as the relationships between these different pathways. These more practical chapters are meant as a compendium for researchers in the field but will also greatly assist those who are new to the subject.

Myxobacteria: multicellularity and differentiation provides a most comprehensive account of these microorganisms, as presented by the world's leading researchers in the field. Diagrams, tables, graphs, photographs and extensive bibliographies complement information in the chapters, and all provided in an easy-to-read format. Furthermore, the book anticipates the progress expected in the different areas of research in the years to come. To paraphrase the book's editor, David E. Whitworth, "the next book on myxobacteria will be able to claim a true understanding of this most complex of prokaryotes".

NICOLE SKINNER
INTERNATIONAL MICROBIOLOGY
nskinner@microbios.org