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Edited by Mohammad R. K. Mofrad and Roger D. Kamm

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CYTOSKELETAL MECHANICS

This book presents a full spectrum of views on current approaches to modeling cell mechanics. The authors of this book come from the biophysics, bioengineering, and physical chemistry communities and each joins the discussion with a unique perspective on biological systems. Consequently, the approaches range from finite element methods commonly used in continuum mechanics to models of the cytoskeleton as a cross-linked polymer network to models of glassy materials and gels. Studies reflect both the static, instantaneous nature of the structure, as well as its dynamic nature due to polymerization and the full array of biological processes. While it is unlikely that a single unifying approach will evolve from this diversity, it is our hope that a better appreciation of the various perspectives will lead to a highly coordinated approach to exploring the essential problems and better discussions among investigators with differing views.

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Cytoskeletal Mechanics

MODELS AND MEASUREMENTS

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Preface

Although the importance of the cytoskeleton in fundamental cellular processes such as migration, mechanotransduction, and shape stability have long been appreciated, no single theoretical or conceptual model has emerged to become universally accepted. Instead, a collection of structural models has been proposed, each backed by compelling experimental data and each with its own proponents. As a result, a consensus has not yet been reached on a single description, and the debate continues.

One reason for the diversity of opinion is that the cytoskeleton plays numerous roles and it has been examined from a variety of perspectives. Some biophysicists see the cytoskeleton as a cross-linked, branched polymer and have extended previous models for polymeric chains to describe the actin cytoskeleton. Structural engineers have drawn upon approaches that either treat the filamentous matrix as a continuum, above some critical length scale, or as a collection of struts or beams that resist deformation by the bending stiffness of each element. Others observe the similarity between the cell and large-scale structures whose mechanical integrity is derived from the balance between elements in tension and others in compression. And still others see the cytoskeleton as a gel, which utilizes the potential for phase transition to accomplish some of its dynamic processes. Underlying all of this complexity is the knowledge that the cell is alive and is constantly changing its properties, actively, as a consequence of many environmental factors. The ultimate truth, if indeed there is a single explanation for all the observed phenomena, likely lies somewhere among the existing theories.

As with the diversity of models, a variety of experimental approaches have been devised to probe the structural characteristics of a cell. And as with the models, different experimental approaches often lead to different findings, often due to the fact that interpretation of the data relies on use of one or another of the theories. But more than that, different experiments often probe the cell at very different length scales, and this is bound to lead to variations depending on whether the measurement is influenced by local structures such as the adhesion complexes that bind a bead to the cell.

We began this project with the intent of presenting in a single text the many and varied ways in which the cytoskeleton is viewed, in the hope that such a collection would spur on new experiments to test the theories, or the development of new theories

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themselves. We viewed this as an ongoing debate, where one of the leading proponents of each viewpoint could present their most compelling arguments in support of their model, so that members of the larger scientific community could form their own opinions.

As such, this was intended to be a monograph that captured the current state of a rapidly moving field. Since we began this project, however, it has been suggested that this book could fill a void in the area of cytoskeletal mechanics and might be useful as a text for courses taught specifically on the mechanics of a cell, or more broadly in courses that cover a range of topics in biomechanics. In either case, our hope is that this presentation might prove stimulating and educational to engineers, physicists, and biologists wishing to expand their understanding of the critical importance of mechanics in cell function, and the various ways in which it might be understood.

Finally, we wish to express our deepest gratitude to Peter Gordon and his colleagues at Cambridge University Press, who provided us with the encouragement, technical assistance, and overall guidance that were essential to the ultimate success of this endeavor. In addition, we would like to acknowledge Peter Katsirubas at Techbooks, who steered us through the final stages of editing.