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978-0-521-15282-2 - Dictyostelium: Evolution, Cell Biology, and the Development of Multicellularity

Richard H. Kessin

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## Dictyostelium

The Dictyostelia are soil amoebae capable of extraordinary feats of survival, motility, chemotaxis, and development. Known as the “social amoebae” or “cellular slime molds,” these organisms have been the subjects of serious study since the 1930s. Research in this area has been instrumental in shaping general views of differentiation, morphogenesis, and communication.

Beginning with the history of Dictyostelids, this book considers the problems of the evolution of this multicellular organism, which is characterized by its ability to transform from a single-celled organism into an elaborate assemblage of thousands of synchronously moving cells. Each stage of this development is treated in a separate chapter. The special properties of the Dictyostelid genome are rigorously analyzed, and the methods available to manipulate genes are presented in detail. Research techniques that enable many cell biology problems to be approached are also presented. Throughout, the emphasis is on combining classical experiments with modern molecular findings, and this book represents the only modern synthesis of such material.

Richard H. Kessin is Professor of Anatomy and Cell Biology at Columbia University.

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*Dedicated to:*

*The Kessins—Galene, Nat, Ruth, Lois, Zach, and Jessica*

*and*

*The Frankes—Gely, Ettaly, and Arva*

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# Dictyostelium

## Evolution, Cell Biology, and the Development of Multicellularity

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## Preface

I was an undergraduate when I first saw a film of *Dictyostelium* aggregating, and decided that it was something I had to study. It would be great to say, 30-odd years later, that I had a clear vision of great issues in biology that could be addressed with such an organism, but actually I just thought it was neat. I suppose it had the correct combination of interest and mystery. Like hundreds, if not thousands of people before and since, I was fascinated by its regularity, its rhythms, and for someone schooled in bacteriophage, it seemed simple. If you are blessed with youth and think *Dictyostelium* development is simple, I hope this book will help you to realize your error without discouraging you.

The thousands who have been taken by this strange little organism include better minds than ours. John Tyler Bonner tells of being a young assistant professor at Princeton who one day received a call to show his slime mold films to Albert Einstein. John showed up with his 16 mm projector and he thinks Einstein and his colleagues were suitably impressed, but he does not actually know. John speaks wonderful French, but Einstein conversed in German.

When I first started to work on this organism, with Maurice and Raquel Sussman at Brandeis University, it was thought remarkable that a eukaryotic organism induced genes and enzymes, just like *E. coli* induced the gene for  $\beta$ -galactosidase. The natural synchrony of development let the Sussmans follow the enzymes responsible for polysaccharide synthesis. Before the advent of cloning, we were limited in our studies of gene induction to adding actinomycin D and cycloheximide, and for many years this was a great frustration. There was a whole counter-school that explained changes in enzyme activity on the basis of substrate fluxes. I remember lots of differential equations. Now, after cloning, Northern blots and RT-PCR, it is assuming to realize that there was

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ever such a conflict, but at the time it was vicious. The book that follows presents quite a lot of history of the field. I hope that readers will find that interesting. I was a history major and perhaps I overemphasize it. Skip it if you like, but Andre Lwoff once said that it is dangerous to parachute young scientists into a new field without some idea of what came before, and I believe him. People in our little field have remarkable longevity, so if you are giving a talk, say, at a conference in 2007, and you have missed the fact that what you are discussing was done by John Bonner in 1957 or Ikuo Takeuchi in 1973, someone is likely to remind you.

Research with *Dictyostelium* has always focused on development, but now that our amoebae have become so amenable to molecular and genetic techniques, they are being used to study a variety of other problems. We can investigate cell motility, transporters, pathogenesis of certain bacteria, or osmoregulation, without ever letting the organisms develop. With the sequencing of the genome, the pace of research will increase. It is already possible to obtain important sequence information from the database. As more interesting sequences appear, my prediction for the future is a greater use of *Dictyostelium* to investigate problems in cell biology. But I am not sure my predictive skills are any better now than they were thirty years ago.

I hope this book will be useful, no matter what the problem under investigation. I have organized it into modules that separate subjects that are normally lumped together. Pattern formation in the mound is separate from the patterning in slugs. These subjects are considered in strict developmental chronology because I think it is less confusing that way. Many of the overlapping roles of the cytoskeleton have been considered separately. Where controversy exists – and there are many – I have tried to point these out. I do not necessarily take a side. In all cases the reader can find the literature, and I hope the book will present the context – if not the solution.

Naturally, I have many people to thank. In addition to the Sussmans, there are my old teachers at Yale – Chris Mathews and Gerry Wyatt. Peter Newell survived my arrogance as a post-doc and has contributed greatly to the current volume. Frank Rothman welcomed me to his laboratory at Brown, and Bill Gelbart was a great friend at Harvard.

For many years it has been my good fortune to work with Jakob Franke, who is good at everything that I cannot do. He has provided the bibliography on which this book is based. Nearly all of the researchers in the field have used his bibliography and realize its value. Jakob has also been the copy-editor of the book, but any mistakes that remain are my fault. There are probably more than a few and I am sure that my friends and colleagues will point out failures due to omission. There are more than 1000 references in the bibliography, but I am sure that I have left out a favorite paper of nearly everyone. I hope there are relatively few factual errors; Jakob has hunted most of them down. I have also to thank Tristan Smith, formerly of the Bronx High School of Science, now an undergraduate at the University of Chicago, for helping me assemble the figures. Ellen Cohen, an undergraduate at Cornell, was also a great help.

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Many people have read chapters. There is enough that is controversial so that no amount of reading can smooth out all errors of emphasis or omission. Nonetheless, there are many people to thank for reading and for supplying figures. These include Bill Loomis, Rob Kay, Larry Blanton, Mark Grimson, Rex Chisholm, Margaret Clarke, Ted Steck, Ted Cox, Alan Kimmel, Steve Alexander, Richard Gomer, Adam Kuspa, Gad Shaulsky and Chris West. The initial chapters were written in the laboratory of Michel Véron and I thank him. Thomas Winckler hunted down the original reference of Brefeld and had photographs made. Carole Parent made invaluable changes in the chapter on aggregation. Herb Ennis, now working with us in what he thinks is semi-retirement, read and corrected the chapter on spore germination. John Bonner, who has much more experience at writing books than I do, read a number of chapters and gave great encouragement. He showed his enthusiasm for research and writing throughout.

The members of my laboratory, Jakob Franke, Herb Ennis, Stefan Pukatzki, Dee Dao, Grant Otto, Mary Wu, and Palma Volino, kept experiments going during this exercise and I thank them. They are probably not looking forward to having me back in the lab. My colleague Gregg Gundersen was a great help with the chapter on motility, as was John Condeelis of the Albert Einstein College of Medicine.

My hope is that this book will help many people use *Dictyostelium* as an experimental organism. I have included a Resources chapter to help with technical details, including media and recipes. The amoebae have a lot to offer and the tools that biologists love – genetics, genomics, biochemistry – are always improving. I have found, over the years, that the major benefit of the organism is the people who work on it. On the whole, we are a remarkably congenial crowd, and our annual meeting has something of the atmosphere of a camp meeting. We all look forward to it, wherever it is. At the last meeting I organized with Greg Podgorski, at Snowbird in Utah, the staff of the resort had recently hosted a conference of Prozac sales people. They thought we were much more fun, and no doubt they were right.

Richard Kessin  
New York, August, 2000