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John Tyler Bonner: The Social Amoebae

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1 INTRODUCTION

Evolution, cell biology, biochemistry, and developmental biology have made extraordinary progress in the last hundred years—much of it since I was weaned on schoolboy biology in the 1930s. Most striking of all is the sudden eruption of molecular biology starting in the 1950s. I will make a reckless generalization that each one of these surges was due to a collision with genetics. Perhaps it would be more accurate to say that they fused rather than just collided, because in each case an extraordinary fruitful symbiosis was the result. First, at the beginning of this century, genetics fused with nineteenth-century cytology, which gave us an understanding of how the genetic material was handled in the chromosomes in mitosis, and particularly in meiosis. Next, genetics fused with Darwinian evolution to give rise to population genetics, a signal advance at the time. Then, with the revolution started by Watson and Crick on the molecular structure of the gene, it was possible, through molecular biology to (1) have a second fusion of genetics with cell biology, making it possible to dissect out the biochemical or molecular events within a cell; (2) to devise a new way of attacking phylogenetic problems

in the study of evolution using molecular-genetic techniques; and finally (3), these new approaches made it possible to dissect out the sequence of molecular steps in development.

I am not done with my generalizations! During all the events I have described, there has been a strong tendency to concentrate on “model” organisms. In the past century there was a tremendous emphasis on *E. coli*, the fruit fly *Drosophila*, and the nematode worm *Caenorhabditis*, but beginning back into the nineteenth century there have been many others that have played a similar role. To mention a few, there was Mendel with his garden peas, followed by other organisms such as maize, amphibian, chick and sea urchin embryos, yeast, myxobacteria, zebra fish, the small plant *Arabidopsis*, and the cellular slime molds. One could add a few more and the list would still be incomplete: for instance, ciliate protozoa (such as *Paramecium*), *Hydra* and other hydroids, sponges, *Volvox* and other algae, myxomycetes or true slime molds, *Phycomyces* and other fungi, mice and other mammals. The degree to which these various examples have been directly affected by genetics and molecular biology varies, but even in those cases where the influence has been small (due to the lack of attention) this is beginning to change. In fact, one can say that it is inconceivable to study the biology today on any organism without genetics and molecular biology. For completeness it should be added that there is now renewed interest in another collision: the realization that evolution and developmental biology are inseparable, something that was already recognized by Darwin.

My reason for using cellular slime molds as an example is that they (along with myself) went through the same evolution from a pregenetic period to one deeply involved in molecular genetics. I have been there to watch every step.

When, as an undergraduate, I began experiments on these slime molds in 1940, only one other person, Kenneth Raper, was working on them at that time. In fact, he discovered the “model” species *Dictyostelium discoideum*, which is the species used in the majority of the experimental work today. His early experiments were in the classic mold of the embryology of that time and are still recognized today as being at the root of all subsequent work.

As a young student at Harvard I developed two great interests. One was the fungi and other lower plants which were the province of my professor, William H. Weston. He was a charismatic teacher who exuded excitement for the possibility that lower (cryptogamic) plants, such as algae and fungi, made ideal subjects for experimental studies. He had many distinguished students, and when I started with him as an undergraduate, one of his finishing graduate students was John Raper, who was making the pioneer discovery of sex hormones in the water mold *Achlya*. Ralph Emerson had made similar significant advances with another water mold, *Allomyces*. While surrounded by these older students and Weston himself, I knew I wanted to be a cryptogamic botanist. But then I took a course in animal embryology with Professor Leigh Hoadley and was suddenly confronted with all the wonderful work of Hans Driesch, Wilhelm Roux, Hans Spemann, Edwin Grant Conklin, Ross Harrison, and many others who had advanced experimental embryology in the nineteenth and early twentieth centuries. I became entrapped all over again—I wanted to become two people. Then one day it dawned on me: why not work on the embryology (or developmental biology as it became to be known later) of lower plants!

To do this I had to find the ideal organism. Because I was surrounded by water mold enthusiasts it was very tempting to choose their area of interest. However, all that changed when one day I found the Ph.D. thesis of Kenneth Raper's (John's older brother), who had done his graduate work with Professor Weston a few years earlier. It described his discovery of *D. discoideum* and those wonderful experiments I mentioned. Here was exactly what I was looking for: the ideal non-animal embryo. I immediately wrote to Kenneth Raper, and he sent me cultures with some gracious encouragement that has kept me going for almost seventy years.

The question of how an egg develops into an adult was a matter of wonder and concern going back to Aristotle, and it blossomed at the end of the nineteenth century and into the twentieth: one could experiment on embryos and discover the causes of the developmental steps—why one stage produced the next. In the 1940s and 1950s it was realized that it was not just the embryos of higher animals and plants that developed, but development was a property of all organisms, from fungi to algae and other lower forms. Now the cellular slime molds showed themselves to be ideally suited for the study of experimental developmental biology. So first, following the tradition of Raper, an interest began not only in the description of the phases of their development, but in experimental studies parallel to those of causal embryology.

At first there was a difficulty because there was no known sexual system for the cellular slime molds. Later, when it was discovered, it turned out to be intractable and did not allow any way to do simple crossing experiments, unlike Mendel's model organism, the garden pea. In the beginning of the attack there were moderately successful ways of getting around

this difficulty, and later, with the arrival of more and more clever molecular techniques, the disadvantage of the lack of ability to do crossing experiments virtually disappeared. The molecular genetics of the developmental biology of *D. discoideum* (which was now simply called *Dictyostelium*, reflecting its newfound status as a model organism) became central. The most recent high point in this program has been the sequencing of its entire genome: now it is possible to find out how many genes we share with a slime mold. The result is that our insights and understanding of the development of *Dictyostelium* have vastly increased.

In this joyous molecular roller-coaster ride there are many things about these slime molds that have to some degree been neglected, therefore stimulating me to write this book. Besides the central role of their development, many other aspects of their biology are equally fascinating, and here I would like to give the whole picture. As we shall see, they have not been ignored but simply overshadowed by the number of workers and publications in molecular developmental biology. Here I want to give all aspects of cellular slime mold biology equal time.

This means I want to give something closer to equal time to their evolution, their ecology, and their behavior, as well as their development. Within these big categories, starting with evolution, I will include discussions of their history on Earth, the taxonomy of the whole group and how they are related to one another, the origin of their multicellularity, and the interesting aspects of their peculiar sociobiology. The discussion of ecology will also involve their distribution in the soil, which is their natural habitat, their geographic distribution, and their mechanisms of dispersal. Concerning

their behavior, besides the mechanism of how individual amoebae come together in the aggregation chemotaxis, two other matters are of major interest: one is the mechanism of locomotion of the migrating slugs, and the other is how slugs orient—what is the mechanism that makes them turn in towards light and sense heat and chemical gradients. More work has been done on aggregation chemotaxis than on any other aspect of slime mold biology; there is a rich literature. Turning to development, one aspect that has been studied in detail is the mechanism of differentiation of stalk cells and spores and how their proportions are controlled. Also there is the interesting question of the ways in which different species differ in their patterns of differentiation. As in all of biology, comparative studies showing differences among species are often helpful for a better understanding of the basic mechanisms; with all its advantages, there is a danger of clinging exclusively to one model organism. Finally, considering the great volume of work these days on the molecular analysis of development, I want to explore in what ways it has shed light on fundamental issues. It has done so, but some of the successes stand out as particularly significant.