

BOOKS: DEVELOPMENT

Model Metaorganism

Graham Bell

You are, let us imagine, given three tasks: to create life, to enclose it in a membrane so as to make a cell, and to glue some cells together to form a multicellular organism. Most people would regard the first task as formidably difficult—certain to take a long time to accomplish, if indeed it could be accomplished at all. The second, although certainly no pushover, looks much less forbidding. And the third is surely rather

trivial: given a functioning cell, it should not be very difficult to form a clump of cells that will give rise to similar clumps.

Our intuition, however, is flatly contradicted by the actual course of events. The remains of cellular organisms have been found in rocks from more than 3400 million years ago (Ma). So life itself, in the form of the first self-replicators, must have arisen rather soon (in geological terms) after the formation of the oceans. There was then a long pause. The enigmatic organism Grypania (up to a meter long but only a couple of millimeters broad) appeared about 2000 Ma. But only after three-quarters of the history of life has passed do we find evidence, in rocks not very far beneath the base of the Cambrian, of algae with massive thalli and body plans more complicated than a filament. Subsequently, multicellular designs have become extremely fashionable, evolving independently in a variety of eukaryotic lineages. The origins of multicellularity and the reasons for the success of multicellular organisms are thus much more difficult and interesting questions than they might appear at first glance.

They are also relatively neglected questions, receiving much less attention than the other great eukaryote enigma, the evolution of sex. Perhaps this neglect can in part be attributed to the model systems chosen by molecular and evolutionary geneticists. Some, like *Escherichia coli* and yeast, are unicellular organisms, and others, such as *Drosophila* and *Arabidopsis*,

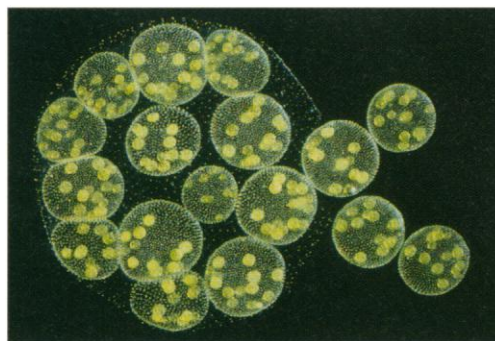
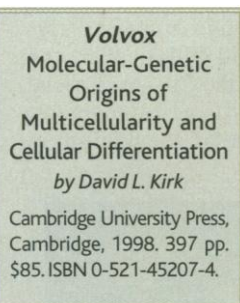
are much larger and more complex. Between these two levels of organization, where one might turn for systems in which to investigate the evolution and genetics of multicellularity, there lies what might be called the “simplicity gap”—the puzzling scarcity of multicellular organisms built of fewer than a thousand cells. There are remarkably few such organisms, and most are unsuitable as model systems because they are obligate parasites (such as dicymid mesozoans), for example, or form part of a life cycle that includes much larger individuals (such as fern gametophytes).

Only one group of organisms seems to satisfy all the criteria for a model system for multicellularity: *Volvox* and the unicellular and multicellular chlorophytes to which it is related. *Volvox* is an integrated multicellular organism showing the simplest kind of cellular differentiation, that between soma and germ. A great deal of relevant background information and a battery of techniques for working with *Volvox* are available from the extensive re-

ganisms, when the normal control of development breaks down, a whole range of bizarre phenotypes appears. (My favorite is the mutation affecting embryonic inversion so as to produce an adult shaped like a doughnut.) Only in *Volvox*, however, can cellular differentiation—and even multicellularity itself—break down completely and still yield viable strains. The complete range of phenotypes found among volvocine algae can thus be re-created in *Volvox* and subjected to genetic analysis. The fairly simple picture now emerging from this analysis shows that three genes are primarily responsible for the initial differentiation of cell type and the subsequent restriction of division to the germ cells. The structure of these genes and their mode of action are beginning to be understood. In time they will provide the first complete account of how a differentiated multicellular creature is assembled.

These achievements are impressive enough, especially given the restricted membership of the *Volvox* research community. The most remarkable feature of Kirk's book, however, is that it transcends conventional genetic analysis to also include evolutionary and ecological analyses. When we speak about mechanism in the context of development, we usually mean something strictly physiological that explains how genes are expressed and how their products react. Only rarely do we consider a quite different category of mechanism, one involving the variation and selection of developmental pathways. Even more rarely is a single author able to present both categories of explanation in the same volume. Kirk

succeeds at this task and gives authoritative accounts of both the molecular genetics of *Volvox* development (where his own contributions have been made) and the evolutionary genetics and ecology of the volvocine algae. He suggests that phylogenetic analysis of the structure and function of the relevant genes in the simpler relatives of *Volvox* will show us how such an organism evolved. Kirk also describes comparative analyses suggesting explanations for the function of multicellularity that can be tested experimentally. This breadth of treatment raises Kirk's book from a technical monograph, read only by specialists, to a synthesis that can be appreciated and enjoyed by any biologist. The book is a progress report on the enterprise that began when van Leeuwenhoek first saw *Volvox* roll into the field of his primitive microscope three centuries ago. It seems the most remarkable work of its kind since John Tyler Bonner's *The Cellular Slime Molds* (1959), and it deserves to achieve the same celebrity.



Volvox multiplying. Juvenile spheroids hatching from their parent.

search on its unicellular relative, *Chlamydomonas*. Its other relatives provide a superb source of comparative data for investigating vegetative and sexual differentiation. *Volvox* is ecologically and genetically convenient. It even contrives to be green and motile at the same time. In short, it provides the best opportunity we know of to investigate the most fundamental aspects of multicellularity.

It is fair to say that this opportunity has not been seized very decisively. Many people have studied *Volvox* at one time or another, but most have moved on to other systems. David Kirk and his collaborators, however, have stuck with the system, and have made it the focus of a major research program. Using mutants in which somatic or sexual organization is disrupted, they have sought to identify and characterize the genes responsible for the development of a multicellular individual that is stable and differentiated. One cannot fail to be fascinated by their results. As in other or-

The author is director of the Redpath Museum, 859 Sherbrooke Street West, Montreal, Quebec H3A 2K6, Canada, and in the Department of Biology, McGill University, Montreal, Quebec H3A 1B1, Canada. E-mail: gbell2@maclean.mcgill.ca

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